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UNIVERSITY OF ALBERTA

ROLES OF COMPETITION AND FOOD SUPPLY IN STRUCTURING AN ANT POPULATION

BY

© RICHARD J. DESLIPPE

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of Doctor of Philosophy

DEPARTMENT OF ZOOLOGY

Edmonton, Alberta
Fall 1994

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Abstract

To understand more clearly patterns of distribution and abundance of ants, I studied resource limitation and intra- and interspecific competition in *Formica podzolica*. First, I examined associations between habitats that differed in food supply and colony abundance, dispersion, productivity, sex investment and size of colony members. In addition, I compared productivity and sex investment of food supplemented and control colonies. Patterns across habitats suggested that food supply has a major role in structuring the ant population. My feeding experiment provided further support for this conclusion, because food supplemented colonies were more productive and more female-biased than control colonies.

Second, I tested whether established colonies, (1) prevent foundresses from starting new colonies near their nests, (2) eliminate small colonies transplanted near their nests, and (3) compete exploitatively for food. A removal experiment failed to produce significant differences in reproductive output and sex allocation between control and neighbour-removed colonies. However, survivorship was significantly affected by interference competition between colonies of *F. podzolica* and three other *Formica* species. Space preemption of founding queens and/or interference between established colonies were key mechanisms in all species but *F. podzolica*. The relative importance of these mechanisms was contingent upon the neighbouring species, and understood in terms of species characteristics, particularly activity levels, aggressiveness and development of recruitment systems.

Finally, I compared development of colonies and survivorship of queens in experimental nests started with 1 to 16 foundresses. Small groups (2 to 4 queens) had less mortality than larger groups (8 or 16 queens), and produced more pupae than larger groups or single queens before the first nests produced workers. Due mainly to both competition and social parasitism, the early stages of colony development represent survivorship bottlenecks. I argue that cooperation among queens is a strategy employed by *F. podzolica* to accelerate development through these stages.

Preface

This dissertation was written as a series of manuscripts around a central theme. When I submitted this dissertation, a version of Chapter 2 was *in press* in the *Journal of Animal Ecology* 63(4).

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CHAPTER 1

INTRODUCTION

A. Overview of chapter

This chapter is organized in four parts. I begin by stating the overall objective of the research reported in this dissertation, and summarize the objectives and findings of the individual studies. I then explain the relationships among the studies to elucidate both why the projects were done and how they are linked. Next, I provide an overview of competition in ecological systems. Finally, I describe the particulars of the study system.

B. Objectives and organization of dissertation

In this dissertation, my objective is to investigate the nature and consequences of both resource limitation and intra- and interspecific competition in organizing a population of *Formica podzolica*. Because body size is frequently a major determinant of the nature, degree and outcome of interactions (Tokarz 1985, Schoener 1986, M'Closkey et al. 1990, Wootton 1993), I emphasize or control for colony size or stage of the life cycle in many comparisons. In social insects, these measures are positively associated and analogous to body size in most other taxa (Oster and Wilson 1978, Hölldobler and Wilson 1990).

In each of four empirical chapters, I address specific questions by combining descriptive, comparative and experimental studies. I begin my study on the theme of competition by explicitly considering the nature and consequences of resource limitation. Then I proceed with an investigation of competitive mechanisms between colonies of *F. podzolica* and those of three other ant species. Finally, I examine an establishment strategy queens may use to accelerate development through the founding stage and early stage of worker production. These stages represent survivorship bottlenecks due mainly to competition and social parasitism.

In chapter 2, I describe associations between habitats that differed in natural food supply and colony abundance, dispersion, productivity and sex investment and size of colony members. In addition, I compared productivity and sex investment of colonies fed and not fed with supplemental food. Patterns across habitats suggested that food supply has a major role in structuring the population of *F. podzolica*. My feeding experiment provided further support for this hypothesis, because food supplemented colonies were more productive than control colonies. My experimental result and those of related studies indicate that species of ants storing little food compared to those storing much food like desert harvester and honey-pot ants are more sensitive to changes in food supply and respond to food addition in the short-term, even within one reproductive cycle.

In chapter 3, I inspect the proximate role of food in determining sex investment by comparing reproductive parameters of colonies and populations across habitats, and comparing sex allocation of food supplemented and control colonies. Reproductive parameters were associated with habitats that varied in natural food abundance. There was a strong tendency for individual colonies to produce either all-male or all-female sexuals, and worker size was greatest in colonies producing all-females and smallest in those producing all-males. Sex investment was greatly affected by a supplemented diet, and investment ratios were more male-biased in polygynous colonies than in monogynous colonies. These results demonstrate that food supply has an important proximate influence on sex investment, and suggest that variation in food resources may account for part, perhaps much, of the great variability in sex investment typical of natural populations of social insects.

In chapter 4, I examine potential mechanisms of competition in four species by testing whether established colonies prevent foundresses from starting new colonies near their nests, whether established colonies eliminate small colonies transplanted near their nests, and whether diffuse competition among established colonies of *F. podzolica* affects sexual production and sex allocation. A removal experiment failed to produce significant differences in reproductive output and sex allocation between control and neighbour-removed colonies. However, space preemption of founding queens and interference between established colonies were key mechanisms in all species examined except *F. podzolica*. The relative importance of these mechanisms was contingent upon the neighbouring species, and understood in terms of species characteristics, particularly activity levels, aggressiveness and development of recruitment systems.

In chapter 5, I document the variation in number of queens occurring naturally in founding, immature and mature nests, and compare development of colonies and survivorship of queens in experimental nests started with 1 to 16 foundresses. In the field, number of queens per nests was associated with stage of colony development and nests were facultatively polygynous. Colonies were usually established by single queens (haplometrosis), but establishment by multiple queens (pleometrosis) also occurred. In laboratory nests, small groups (2 to 4 queens) produced more pupae than larger groups (8 or 16 queens) or single queens once the first nests produced workers. Although foundresses usually cooperated and cohabited peacefully, they were often hostile in large groups. Foundresses in pleometrotic nests lost more weight and suffered greater mortality due to antagonistic behaviour compared to single foundresses. Finally, rate of queen mortality correlated positively with initial number of queens in a nest, and was constant throughout the study, except when I maintained temperature at 5°C. Due in part to both competition and social parasitism, the early stages of colony development represent survivorship bottlenecks. I argue that pleometrosis is a strategy employed by *F. podzolica* to accelerate development through these stages.

In the last chapter, I present a synopsis of the research presented in this dissertation, indicate the significance of the findings, speculate on the dynamics of the study system and elaborate on follow-up questions that could be addressed.

C. Rationale and links among studies

Ecologists are fundamentally interested in understanding what determines distribution and abundance of organisms. Competition, although only one of many determinants, is one of the most studied phenomena in nature, largely because it has a central role in ecological and evolutionary theory. Most field experiments on competition have been designed to address simply whether it occurs. Only in the last decade has there been a concerted effort to address second generation questions like how and why competitive abilities differ between species and habitats (Goldberg and Barton 1992, Gurevitch et al. 1992).

The motivation for the research reported in this dissertation stemmed from a desire to understand mechanisms of interactions in different species combinations. I examined this problem in ants because they are superb subjects for ecological investigation. They are well suited as study organisms, for they are abundant, territorial, easily observed and marked, and key components of terrestrial communities. Most important, they can be manipulated experimentally at the levels of both the colony and individual.

Not all ants are equally suited for addressing particular questions on the nature of competitive interactions. For example, desert harvester ants are excellent subjects for examining foraging behaviour and worker-worker interactions, because their seed resources are easily quantified. However, they make poor subjects for investigation of within colony dynamics, as it is extremely difficult to excavate their nests. I elected to study *F. podzolica* for four main reasons: (1) colonies are conspicuous and very abundant locally, and hence they are readily located, convenient to study and important components of the boreal ecosystem; (2) colonies are easily excavated, and thus, data collection on important variables like production of sexuals and queen numbers per nest is facilitated; (3) colonies are readily cultured in artificial nests. As a result, study of colony founding dynamics is straightforward. Finally, *F. podzolica* and its close relatives are hosts of nearly all parasitic formicines (further details on this interaction are provided later in the chapter), and therefore, they are central to understanding the ecology of social parasites.

In Fig. 1.1, I present an outline of the hierarchy of questions addressed in this dissertation. I start with a consideration of the role of food supply because any study of a population or community should consider resources (Price 1984), resource limitation should be shown before attributing results to competition (Keddy 1989), and food supply appeared *a priori* to be a key limiting factor in at least some habitats. To examine the relationship between food resources and sexual production, I had to collect data on production of both males and females. It was a simple matter, therefore, to consider these individual components and investigate the association between food resources and sex investment. I treated this matter in a separate chapter because it is of special theoretical interest.

After clarifying the relationships between food supply and variables linked to reproductive parameters, it was apparent that the degree of food limitation was habitat dependent. Since food was limiting, it was reasonable to suspect that competition for food was an important process structuring the population. Therefore, I conducted three field experiments to test for competition, and to decipher mechanisms of competition. In this study, I expanded the scope to include both intraspecific and interspecific interactions, because I wanted a more thorough picture of the forces acting on the population of *F. podzolica*.

From this work and the results of other projects (Savolainen and Deslippe unpublished), it was apparent that the founding and early ergonomic stages represent survivorship bottlenecks due largely to both competition and social parasitism. Because these stages are so critical to a colony, I was interested in uncovering strategies *F. podzolica* may employ to develop through them as rapidly as possible. One strategy involves cooperation of queens during colony foundation. In the final project, therefore, I examined the dynamics of this interaction from the establishment stage to the production of the first workers.

In each empirical chapter, I used a combination of descriptive, comparative and experimental studies. By doing so, I capitalized on the strengths and compensated for the weaknesses of each method. A further consequence of this pluralistic methodology was that my conclusions were supported by multiple lines of evidence.

D. General framework

The relative importance of density-independent (e.g., temperature, harsh weather and fire) and density-dependent (e.g., food supply, competition and predation) factors in determining abundance of plants and animals is controversial (Bakker 1964, Klomp 1964, Solomon 1964, Clark et al. 1967, Begon and Mortimer 1981). Andrewartha and Birch (1954) popularized the view that density-dependent factors play a minor, or even no role in determining population size. In contrast, Nicholson (1933, 1954a,b, 1957, 1958) argued that these factors played the main role. The issue has been debated furiously, largely because the protagonists held extreme positions and argued at cross-purposes (Varley et al. 1975, Begon and Mortimer 1981).

A particularly useful outcome of the debate was to clarify the need for distinguishing clearly among the terms determination, regulation and control of population size or other attributes of population structure like spatial distribution, reproductive productivity and sex ratio. Determination of abundance is the result of the combined effects of all factors and processes impinging on a population, whereas regulation means the tendency to return to equilibrium density following any departure from this level due to negative feedback processes. The term control has produced confusion because it has been used both for processes causing change and for those causing regulation (Varley et al. 1975, Begon and Mortimer 1981).

By these definitions, it follows that density-independent processes can determine, but only density-dependent ones can both determine and regulate population size. Most populations are probably regulated at least to some extent since observations of extinctions and catastrophic outbreaks occur less often than expected by chance (Klomp 1962). Although density-dependent processes sometimes do not explain the size of particular populations (Davidson and Andrewartha 1948a,b, Kingsolver 1989, Andrews 1991), often they do (Quinnell et al. 1990, Arcese et al. 1992, Hudson et al. 1992, Massot et al. 1992, Woiwod and Hanski 1992). Consequently, there has been and continues to be great interest in these processes, especially competition (Hassell and May 1990, Van Buskirk and Smith 1991, Barlow 1992, Byers et al. 1992, Hastings 1992, Lawler and Morin 1993, Wissinger and McGrady 1993).

The large body of empirical and theoretical studies on competition address how the process affects population and community structure and the evolution of competitive ability (reviews by Connell 1983, Schoener 1983, Fowler 1986, Keddy 1989, Aarssen and Epp 1990, Goldberg and Barton 1992, Gurevitch et al. 1992). Conclusions on the role and importance of the process in nature are based on evidence derived from descriptive, comparative and experimental studies (Diamond

1986, Keddy 1989). In the first two approaches, competition is inferred from patterns found in data sets gathered from one or more populations or communities (Keddy 1989). These inferences are problematic, however, because identical patterns can be generated from more than one plausible hypothesis (Strong et al. 1984). In the last approach, the possibility of indirect interactions does not eliminate the problem completely (Holt 1977, Bender et al. 1984, Connell 1989), but it is minimized as the independent variables are controlled directly. In addition, properly designed experiments allow rigorous testing that maximizes the possibility of falsifying hypotheses (Strong et al. 1984, Keddy 1989). Therefore, experiments have become increasingly important in the study of competition (Connell 1983, Schoener 1983, Goldberg and Barton 1992, Gurevitch et al. 1992).

Most field experiments on competition have been conducted to address whether it occurs (Goldberg and Barton 1992), but more refined questions include: (1) How and why does the importance of competition vary over space and time? (2) To what extent does competition affect relative abundances and diversity within and across habitats? (3) How and why does competitive ability differ between species and habitats? And (4) what is the relative intensity of intra- to interspecific competition? These questions remain largely unresolved (Goldberg and Barton 1992, Gurevitch et al. 1992), and recent reviews have clarified the need for further experimentation (1) on intraspecific competition, (2) in underrepresented systems like terrestrial arthropods, (3) using larger sample sizes and more complicated designs than most previous studies, and (4) using proper designs and analyses (Hurlbert 1984, Underwood 1986, Hairston 1989, Keddy 1989, Goldberg and Barton 1992, Gurevitch et al. 1992).

In theory, the importance of both intra- and interspecific competition should depend on trophic position (Hairston et al. 1960) and particular attributes like body size (Schoener 1986). Among trophic levels, competition should be more prevalent in autotrophs, decomposers and carnivores, compared to herbivores. This conclusion is based on the premise that autotrophs, decomposers and carnivores are limited by the amount of solar energy, the quantity of dead tissue and the supply of herbivores, respectively, whereas herbivores, occupying an intermediate position in the food web, are more likely to be regulated by predators (Hairston et al. 1960). Within trophic levels, the importance of competition should be greater in larger organisms since they are generally long-lived and resist predation (Schoener 1986).

Organisms that are large, long-lived, secondary consumers and, in turn, resist predation may connote carnivorous vertebrates. However, these traits also characterize the social insects (i.e., ants, termites, and some bees and wasps). First, social insects are large in the sense that many individuals collectively form a reproductive unit, the colony. For example, colonies typically contain 1 000 to 100 000 members and exceed 1 000 000 in some species (Wilson 1971, Hölldobler and Wilson 1990). Second, they are long-lived, with individual queens surviving up to 20 or 30 years and colonies persisting considerably longer. Indeed, colonies of some species are potentially immortal because new queens regularly supersede their dead or aging mothers (Wilson 1971, Hölldobler and Wilson 1990). Third, they consume vast quantities of food that often includes considerable animal prey (Brian 1983, Grant and Moran 1986, Otis et al. 1986). For instance, colonies of the ants *Myrmica laevinodis* and *M. ruginodis* consume between 40 and 80 g of arthropods per m^2 of grassland habitat during the growing season (Petal 1967), a consumption of about 5 000 to 10 000 items each roughly the body size of a medium-sized ant (Petal et al. 1971). Finally, although foraging workers frequently succumb to predation (de Bruyn et al. 1972, Porter and Jorgenson 1981, Whitford and Bryant 1979, Mackay 1982), the colony itself is resilient for the sterile members shelter and aggressively defend their queens (Wilson 1971, de Bruyn et al. 1972, Hölldobler and Wilson 1990).

Competition within and between species, therefore, should and does predominate in social insects (Wilson 1971, Schoener 1983, Jeanne and Davidson 1984, Hölldobler and Wilson 1990). Compared with other social insects, it has been studied more frequently and in greater detail in ants (reviews by Levings and Traniello 1981, Hölldobler and Wilson 1990). The evidence is complex and multifaceted, and comes mainly from (1) dispersion patterns of nest sites (Levings and Traniello 1981), (2) dispersion patterns of species within local communities in body size, foraging activity and prey type (Bernstein 1974, Whitford 1978, Chew and Chew 1980, Chew and DeVita 1980), direct observation of interaction between workers (Mabelis 1979, Möglich and Alpert 1979, Hölldobler 1986, Banks and Williams 1989, Savolainen 1991) and (4) experimental removal or addition of ant colonies (Brian 1952, Bradley 1972, Pontin 1969, Davidson 1985, Rosengren 1986). However, despite the many studies, much remains to be learned about mechanisms of competition in social insects, and how the process affects colony and population structure. As for the more general case, appropriate experimental studies are especially needed.

E. Study system

Ants belong to the family Formicidae within the order Hymenoptera. The known living members of this family comprise 11 subfamilies, 297 genera and 8 800 species (Hölldobler and Wilson 1990). Some genera and many species, however, remain unrecognized. Based on the rate of new discoveries in the last few decades, Hölldobler and Wilson (1990) estimate over 350 genera and 20 000 species may exist in the world. Ants are most abundant in tropical regions, but are also common in nearly all other terrestrial environments ranging from the arctic circle to southern Tasmania and Tierra del Fuego. For example, over 170 species occur in an area of 2.6 km^2 in Papua New Guinea (Wilson 1959), over 20 million individuals are found per hectare in the Ivory Coast Savanna (Lévieux 1982) and over 300 million members compose a single 'supercolony' occupying an area 2.7 km^2 in the Ishikari Coast of Hokkaido (Higashi and Yamauchi 1979). Native species are absent only in Antarctica, Iceland, Greenland, Polynesia east of Tonga, and a few remote islands in the Atlantic and Indian oceans (Hölldobler and Wilson 1990).

The numerical success of ants is largely a product of their advanced social system, technically termed eusociality. Eusociality is the condition under which colony members cooperate in caring for the young, divide labour between reproductive and sterile individuals, and overlap in at least two generations (Wilson 1971). It has lead to great coordination of activities like foraging and defense among colony members that has permitted both exploitation of a wider range of prey and defense against more potential enemies than solitary individuals achieve. Eusocial behaviour has evolved only an estimated twelve times in the Hymenoptera and once in the protoblattoid line that lead to the Isoptera (Wilson 1971, Michener 1974).

Ants are the only eusocial insects that are both predators and nest in soil or ground litter. Contamination presents a major barrier to nesting in moist soil, because it contains many microorganisms. Ants have solved the problem of contamination, though, by evolving a metapleural gland that produces phenylacetic acid, a compound active against fungi and bacteria. The gland is closest to being a single diagnostic character separating the Formicidae from other Hymenoptera (Hölldobler and Wilson 1990).

In eusocial Hymenoptera, males and females develop from unfertilized and fertilized eggs, respectively. This mode of sex determination is termed haplodiploidy, since unfertilized eggs are haploid, and fertilized eggs are diploid (Crozier 1971, Slobododchikoff and Daly 1971). Sex is determined by the number of sex-determining genes on chromosomes, and haploid individuals are male, because they contain only one set of sex-determining genes. Although a colony contains either no males or only a single male caste, it usually has at least two female castes, queens and workers. Queens are reproductive specialists whereas workers are labour specialists. (Wilson 1971).

Whereas sex determination is genetic, caste determination is due to physiological factors. Six factors have been identified as affecting whether a female individual becomes a worker or queen: larval nutrition, temperature, egg size, winter chilling, age of queen and caste self-inhibition (Brian 1979, 1985, de Wilde and Beetsma 1982, Nijhout and Wheeler 1982, Wheeler 1986, Hölldobler and Wilson 1990). Multiple controls exist, and the timing of worker-queen differentiation depends on the species, and varies from 72 hours of egg hatching to about a week before larval growth ceases (Plateaux 1971, Passera 1980, Hölldobler and Wilson 1990).

Haplodiploidy has several effects (Andersson 1984) including those on sex investment due to relatedness asymmetries among workers, males and queens. Trivers and Hare (1976), by combining the theories of kin selection (Hamilton 1964) and sex ratio (Fisher 1958), explained that haplodiploidy creates relatedness asymmetries among colony members, and these asymmetries lead to parentoffspring conflict over sex investment. Specifically, workers are more closely related to their sisters (r = 3/4) than their brothers (r = 1/4), since sisters share on average one-half of the genes they receive from the queen plus all genes they receive from their father, but share with their brothers only one-half of the genes from their mother. Furthermore, the mother (i.e., queen) is symmetrically related (r = 1/2) to both her male and female offspring as in diploid organisms. Consequently, workers strive for a 3:1 female-biased ratio of sex allocation and queens strive for a 1:1 ratio.

Ants have three distinct parts to their colony life cycle (Oster and Wilson 1978). In the founding stage, mated queens establish new colonies either with or without workers (i.e., swarming or independent foundation). Establishment by swarming is common in polygynous species (Keller 1991), and is the sole mode in army ants (Schneirla 1971). In most other ants, though, independent foundation predominates. Following the founding stage is the ergonomic phase, in which the colony allocates most of its energy to producing new workers. This phase is characterized by exponential growth persisting for a few months to many years depending on the species (Hölldobler and Wilson 1990). In the last part of its cycle, the reproductive stage, the colony produces alate sexuals that eventually leave the nest to disperse and mate.

The genus *Formica* is a large and complex group distributed throughout the holarctic, and it is the largest genus of ants in North America (Gregg 1969). The sting has been lost in formicine ants, and has been replaced with an acid-projecting system of which the acidopore is the orifice. Formicine habits include slave-making, temporary social parasitism and various methods of nest construction and colony foundation. In slave-making species, armies of workers raid colonies of host species, and return the brood they steal to their nests. The brood develops into 'slaves' that perform for the slave-makers functions they would normally do for their parental colony. In temporary social parasites, newly fertilized queens penetrate a host colony and kill the host queen. The parasitic queens and the broods they produce are adopted and cared for by the host workers. Both the parasites and their hosts are superb subjects for ecological investigation for they are abundant, territorial, easily observed and marked, and key components of terrestrial communities. Most important, though, they can be manipulated experimentally at the levels of both the colony and individual.

Formica podzolica is a numerically dominant formicine in North America, and is the host of many species of slave-makers and temporary social parasites (Francoeur 1973). Compared to most other host species, *F. podzolica* is an aggressive ant. However, it is timid relative to most species in the exsecta, rufa and raptiformica complexes (Wheeler and Wheeler 1986, personal observations). Mature colonies may exceed 100 000 workers and they make conspicuous earthen mounds. Workers tend aphids for their carbohydrate excretions and prey on various invertebrates. Francoeur (1973) considers *F. subsericea*, *F. glacialis* and *F. podzolica* to be separate species, and I have followed his classification. Wheeler and Wheeler (1986), however, consider *F. glacialis* and *F. podzolica* to be synonymous with *F. subsericea*.

I conducted field work in Elk Island National Park (53° 37' N, 112° 58' W), Alberta, Canada, from 1990 to 1993. The Park covers 195 km^2, ranges in elevation from 710 to 755 m above sea level and represents the transition between the boreal mixed-wood forest of northern Alberta and the grasslands of the south. Most of the Park is composed of trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) forests, and the remainder is wetlands, boreal mixed-wood forests, sedge meadows, shrublands and grasslands. Some common shrubs and forbs in the Park are beaked hazelnut (*Corylus cornuta*), wild rose (*Rosa acicularis*), wild red raspberry (*Rubus strigosus*), goldenrod (*Solidago* spp.) and fireweed (*Epilobium* spp.).

My study sites were located along the edges of the aspen-poplar forests and in grazed and overgrazed meadows. For convenience, I refer to the forest edge and the meadows as 'habitats' throughout the dissertation, although the meadows are actually one type of habitat that differ in grazing intensity. Grazing pressure by ungulates, especially bison (*Bison bison*), was similar along forest edges and in grazed meadows, but it was clearly greater in overgrazed meadows where large herds of bison fed daily. On all study plots, the soil was either an orthic or dark gray luvisol (Crown 1977) and the vegetation was mainly grasses and a few shrubs.

Formicine ants are very abundant in the Park, and they rank from most to least abundant as follows: *F. podzolica* (host of all slave-makers and temporary social parasites), *F. subnuda* (slave-maker), *F. dakotensis* (temporary social parasite), *F. ulkei* (temporary social parasite), *F. subintegra* (slave-maker) and *Polyergus breviceps* (slave-maker). *Formica podzolica* is readily distinguished from the parasitic species because it is a large black ant, whereas the parasites are large red ants.

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WHAT ARE THE MAJOR DETERMINANTS OF DISTRIBUTION AND ABUNDANCE OF *F. podzolica*?

Is food limiting?

- ***What variables are affected?***
  - *Across populations*
    - abundance
    - dispersion
    - productivity
    - sex ratio
    - sex allocation
    - worker size
    - size of sexuals
  - *Across colonies*
    - productivity
    - sex ratio
    - sex allocation
    - worker size
    - size of sexuals
    - mass of sexuals
    - foraging radius
  - *Within colonies*
    - sex allocation
    - number of queens

Is food limitation habitat dependent?

Are patterns a product of competition among colonies?

- ***What are the mechanisms of competition?***
  - *Intraspecific*
    - diffuse competition
    - space preemption
    - interference among colonies
  - *Interspecific*
    - space preemption
    - interference among colonies

Is nature and outcome of competition dependent on degree of size asymmetry?

What are consequences of survivorship bottleneck?

- ***Colony founding strategies***

What are dynamics of the study system?

- ***Speculations***

Fig. 1.1. Outline of hierarchy of questions addressed in this dissertation.

CHAPTER 2

ROLE OF FOOD SUPPLY IN STRUCTURING AN ANT POPULATION

A. Introduction

A major goal of ecology is to identify determinants of distribution, abundance and productivity of individuals. Food supply often has a large effect on these measures (Lack 1954, Martin 1987, Boutin 1990), but other factors like weather, predation or territorial behaviour may keep densities well below those at which food shortages occur (Andrewartha and Birch 1954, Sinclair 1989, Arcese et al. 1992). When this happens, additional food should have little or no effect on individuals and populations. To determine whether food is limiting, ecologists have searched for correlations between abundance, distribution and productivity of individuals and food supply (Power 1984, Gee 1988, Butynski 1990), or have added food and compared the dynamics of populations with and without food added (Boutin 1990, Simons and Martin 1990, Klenner and Krebs 1991, Richardson 1991).

Food supply should have a major effect on colonies and populations of social insects (i.e., ants, termites and some bees and wasps), because colonies of these insects are often long-lived, populous and locally abundant. However, the role of food supply on abundance, distribution and productivity of colonies has been only sparsely documented compared to the role of other factors, especially territorial aggression (Hölldobler and Wilson 1990). Most investigations of whether social insects are food limited have simply involved the association of patterns of these measures with perceived levels of food (reviews by Jeanne and Davidson 1984, Hölldobler and Wilson 1990). Although the associations have been reasonable, there has been little attempt to measure food supply directly. Few studies have manipulated food supply experimentally by feeding colonies (Munger 1992) or adding (Pontin 1969) or removing neighbours (Davidson et al. 1985), and then evaluating the treatment effect on either total alate production or colony density. Field experiments performed to date have been done mainly with ants, and they have led to conflicting results. Those conducted with temperate grassland or forest species have usually generated clear, short-term, treatment effects (Pontin 1961, 1969, Yasuno 1965, Backus and Herbers 1992). In contrast, experiments with desert harvester species usually have produced marginal (Ryti and Case 1988) or non-significant effects (MacKay 1981, Davidson et al. 1985, Munger 1992).

Despite a possible exception (Davidson et al. 1984), a key difference between experimental studies showing clear, short-term, treatment effects and those that do not may be the extent to which the species involved store food. Harvester ants, especially those of the genus *Pogonomyrmex*, are known to store food in quantity (MacKay and MacKay 1984, Vander Wall 1990), and this storage may moderate or militate against changes in colony density or alate production due to a surplus or shortage of food in the short-term. In contrast, temperate grassland and forest ants store relatively little food directly (Vander Wall 1990), and therefore, they may be more sensitive to changes in food supply, and may respond to these changes even within one reproductive cycle.

In this chapter, I address the issue of food limitation in the ant, *Formica podzolica*, a temperate grassland species that does not store food directly to any great extent (personal observation). I have four objectives: (1) to compare patterns of colony abundance, distribution and reproductive output, and sizes of males and females along forest edges and in grazed and overgrazed meadows; (2) to determine how differences among the habitats in these variables correlate with natural food supply; (3) to determine experimentally whether reproductive output of colonies is limited by food, and if so, whether addition of food results in increased productivity of sexuals, relative to controls, within one reproductive cycle; (4) to compare productivity of sexuals between colonies fed in overgrazed meadows (the poorest habitat) and those of unfed colonies along forest edges (the best habitat).

Study area

I conducted field work in Elk Island National Park (53° 37' N, 112° 58' W), Alberta, Canada, from 1990 to 1993. The Park covers 195 km^2, ranges in elevation from 710 to 755 m above sea level and represents the transition between the boreal mixed-wood forest of northern Alberta and the grasslands of the south. Most of the

Park is composed of trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) forests, and the remainder is wetlands, boreal mixed-wood forests, sedge meadows, shrublands and grasslands.

My study sites were located along the edges of the aspen-poplar forests and in grazed and overgrazed meadows. For convenience, I refer to the forest edge and the meadows as 'habitats' throughout the text, although the meadows are actually one type of habitat that differ in grazing intensity. Grazing pressure by ungulates, especially bison (*Bison bison*), was similar along forest edges and in grazed meadows, but it was clearly greater in overgrazed meadows where large herds of bison fed daily. On all study plots, the soil was either an orthic or dark gray luvisol (Crown 1977) and the vegetation was mainly grasses and a few shrubs. Further details on the study sites are provided in Chapter 1.

Formica podzolica is widely distributed in North America (Francoeur 1973) and is the numerically dominant *Formica* ant in Elk Island National Park. It is a medium-sized, black ant that nests primarily in soil and forms conspicuous earthen mounds, the largest of which exceed 2 m in diameter. I estimate that colonies producing alate sexuals typically contain 5 000 to 40 000 workers, and the largest ones exceed 100 000 workers. Workers tend homopterans for honeydew, and they scavenge and prey on a wide variety of invertebrates from March to October. The sexuals leave their nests from late July to early September to mate, and thereafter, males die, and females try to initiate new colonies.

B. Materials and methods

Surveys

I surveyed a total of 15 plots along forest edges and in grazed and overgrazed meadows to compare the density and dispersion of *F. podzolica* nests within and among these habitats. Because I desired relatively homogeneous plots within a habitat, with each containing at least 20 nests, the area of my plots ranged necessarily over two orders of magnitude across habitats (Table 2.1). To reduce any problems of scale in comparisons among habitats, I selected the five plots in each habitat with the greatest density of nests based on a search for suitable plots over an area of about 50 km^2. In each survey, I measured the length and width of each nest and the distance to the nest of the nearest conspecific neighbour. I conducted the surveys in 1991 and 1992, prior to the first mating flight of the year.

Headwidths and body mass

I measured the headwidth (a standard measure of body size in ants) of alate sexuals of *F. podzolica* from 148 colonies along forest edges and in grazed and overgrazed meadows to compare size among habitats and between sexes. For each colony, I measured the headwidth of either 30 males or females. The colonies were sampled in July of 1991 and 1992 prior to the first mating flight of the season.

I measured the fresh mass of alate sexuals of *F. podzolica* to compare body mass between sexes, and to use the values for each sex in calculations of reproductive output. I sampled 30 colonies in July of 1992, and measured the total mass of either 30 live males or females on the same day I collected the samples.

Productivity and food supply

To compare production of sexuals by colonies across habitats, I excavated 150 nests of *F. podzolica*, 50 each along forest edges and in grazed and overgrazed meadows. I selected colonies haphazardly, without prior knowledge of their current investment in sexuals. I excavated the nests along forest edges and in grazed meadows in 1991 and those in overgrazed meadows in 1992. In both years, I conducted the excavations in July, prior to the first mating flight of the year. Before an excavation, I measured the maximum and minimum diameter of the mound at ground level and used these values to calculate what I refer to, hereafter, as nest area (in cm^2) by the equation of an ellipse:

$$\pi(ab)/4 \qquad (1)$$

where a and b = maximum and minimum diameter of mound, respectively. I counted all alate sexuals in each colony and determined reproductive output (in grams) by the equation:

$$(\text{Number of males} \times 0.0182) + (\text{Number of females} \times 0.0314) \qquad (2)$$

where the values 0.0182 and 0.0314 are the mean fresh masses of males and females in grams, respectively (see Results).

I estimated the natural supply of invertebrates in April, May and June, 1992, in the three habitats. In each month and scattered throughout each habitat, I set in the ground 25 circular pitfall traps (diameter = 11 cm) containing water and dish soap in the ground. I collected the traps after 4 d (3 d in May) and counted the number of invertebrates in each container. Thirty-two of the 225 traps were either lost or destroyed by bison.

Food-addition experiment

I conducted a food-addition experiment in 1992 in overgrazed meadows to determine whether colonies of *F. podzolica* were limited by food. I did the experiment in overgrazed meadows because they were a relatively poor habitat for *F. podzolica*. In March, I selected 50 control and 50 treatment colonies scattered throughout overgrazed meadows and placed a small rock labelled with a unique mark on the top of the mound to identify the nest. I fed each treatment colony both tuna and honey 50 times from April to July. I distributed the tuna by scattering it in small pieces on and around the mound, and poured undiluted, liquid honey on a rock that I had placed initially on each control and treatment colony. The colonies were fed *ad libitum*; overall, I provided about 34 kg of tuna and 4 L of honey. Most of the food was consumed by the treatment colonies. Vertebrates did not eat the food, but workers of neighbouring colonies of *F. podzolica*, and *Myrmica* spp. consumed some honey and brought small quantities of tuna to their nests.

i) Productivity

To compare production of sexuals by control and treatment colonies, I excavated the colonies in July, 1992, prior to the first mating flight of the year, and counted the alate sexuals. I determined nest area and reproductive output in the same manner described previously.

ii) Foraging distances

To determine whether addition of food affected the foraging distance of workers, I compared the maximum foraging distance of workers from 10 control and 10 treatment colonies in June, 1992. I observed foraging workers from each colony for up to an hour and measured their maximum distance from the nest. To confirm the colony of origin, I gave the worker a small chironomid and followed the homing ant.

Data analysis

I report descriptive statistics as means ± one standard error. I used standard inferential statistics to analyze data when variances were homogeneous by the F_{MAX} test (Sokal and Rohlf 1981). Prior to all parametric analyses, except for data on headwidths, I transformed the data using a log (x) or a log (x + 1) transformation. I performed all analyses on a computer using the SAS (1987) statistical package.

I determined the dispersion pattern of nests on each study plot using the nearest-neighbour measure of Clark and Evans (1954). The dispersion index, R, ranges from 0, indicating perfect aggregation, to 2.1491, indicating perfect hexagonal uniformity. An R of 1 indicates random dispersion. I tested the statistical significance of R using the Z transformation and tested the null hypotheses of no difference in dispersion values, density and nearest-neighbour distances among habitats with Kruskal-Wallis tests. To locate the significant differences in the Kruskal-Wallis analyses, I applied a Tukey-type multiple comparison test (Zar 1984).

Using two-way ANOVA's and Tukey's multiple comparison tests, I tested the null hypotheses of no difference in headwidths between males and females and among habitats, and no difference in food supply among months and among habitats. With ANOVA, I tested the null hypotheses of no difference in fresh mass between males and queens, and no difference in maximum foraging distance. Finally, I used ANCOVA to test the null hypotheses of no difference in reproductive output among habitats, between fed and control colonies and between fed colonies and unfed colonies located along forest edges.

C. Results

Surveys

Nests of *F. podzolica* were dispersed uniformly on all plots along forest edges, and dispersed either uniformly or randomly on plots in grazed and overgrazed meadows (Table 2.1). Dispersion values (R) differed significantly among habitats ($H = 10.22$, $df = 2$, $P < 0.006$) and were more uniform along forest edges. The only significant pairwise comparison of R was between forest edge and grazed meadow ($q = 4.40$, $P < 0.01$).

Both nest densities and nearest-neighbour distances between nests differed significantly among habitats (Table 2.2). Density was highest along forest edges and lowest in overgrazed meadows, whereas nearest-neighbour distance was shortest along forest edges and longest in overgrazed meadows. For both density and nearest-neighbour distance, the only significant pairwise comparison was between forest edge and overgrazed meadow ($q = 4.90$ for both variables, $P < 0.005$).

Headwidths and body mass

Females weighed significantly more than males ($F_{1, 29} = 620.58$, $P < 0.0001$). Mean mass of individual females and males was 31.4 ± 0.3 mg and 18.1 ± 0.4 mg ($n = 15$ colonies for both sexes), respectively. Similarly, females had significantly larger headwidths than males (Table 2.3). However, headwidths of neither males nor females differed among habitats. The interaction of sex and habitat was not significant (Table 2.3).

Productivity and food supply

Alate production of colonies differed significantly among habitats (Fig. 2.1), being greatest along forest edges and lowest in overgrazed meadows. All pairwise comparisons of reproductive output between habitats were significant by the method of least-squares means (forest edge vs. overgrazed meadow: $P < 0.0001$; forest edge vs. grazed meadow: $P = 0.0065$; grazed meadow vs. overgrazed meadow: $P = 0.015$).

I collected 20 984 invertebrates in 193 pit-fall traps. The number of invertebrates per trap per day differed significantly both among habitats and among months and there was a significant habitat by month interaction (Fig. 2.2). The abundance of invertebrates was always greatest along forest edges, but not significantly so in June. It was lowest in overgrazed meadows in April and May but lowest in grazed meadows in June (Fig. 2.2).

Food-addition experiment

Fed colonies produced significantly more alates than control colonies (Fig. 2.3). The maximum foraging distance of workers did not differ between fed and control colonies ($F_{1,19}$ = 0.04, P = 0.84; means were 10.03 ± 1.21 m and 10.32 ± 0.74 m, respectively; n = 10 for each). Alate production did not differ significantly between fed colonies in overgrazed meadows and unfed colonies along forest edges (Fig. 2.4).

D. Discussion

In this chapter, I addressed the issue of food limitation in an ant population by presenting multiple lines of evidence, both experimental and non-experimental. Unlike most related studies, the evidence was based on large sample sizes. I felt this sampling effort was necessary to address the issue properly because of the inherent variability of many measures associated with ant populations (Hölldobler and Wilson 1990). My results show that food supply has an important role in determining distribution, abundance and productivity of colonies of *F. podzolica* in both the short- and longer-term. First, patterns of colony abundance, distribution and reproductive output differed across habitats that differed in natural food levels. Second, colonies responded to food supplementation within one reproductive cycle by increasing production of alate sexuals.

Food supply and abundance and distribution of colonies

I measured food levels in three different months of only one year. However, I believe patterns of food supply among habitats would be similar among years because, in general, abundance and diversity of invertebrates are greater along ecotones and in habitats with greater structural complexity (Petrusewicz 1967, Boomsma and van Loon 1982). In Elk Island National Park, the overgrazed meadows are used annually by bison as their mating grounds, and the heavy grazing pressure results in little structural complexity relative to forest edges and grazed meadows.

Although the differences among habitats in abundance and distribution are associated with food supply at least in early spring, the main determinant of abundance and distribution could be some other key feature that may differ among habitats. An obvious difference besides food is differential disturbance by bison among habitats. Bison grazed in all three habitats regularly, but they occupied the overgrazed meadows most often. Excessive disturbance by bison may affect colonies of *F. podzolica* directly or indirectly in ways other than indirect effects on food supply, but I have no data to address this issue.

Many studies on social insects have described patterns of abundance and distribution of colonies (Levings and Traniello 1981, Boomsma et al. 1982, Adams and Levings 1987, Cushman et al. 1988). Results depend on the spatial scale of the study areas (Pielou 1977), and most investigations, including this one, have been done within fairly homogeneous patches. As did my study, these studies generally showed that in areas of high colony density, colonies tend to be dispersed uniformly, but in areas of lower density they tend to be dispersed randomly. This pattern is usually interpreted as being the product of intra- or interspecific competition (Levings and Traniello 1981), of which one possible mechanism is exploitative competition for food. Sometimes differences in food supply between or among sites are inferred (Brian 1979), but rarely has food supply been measured directly (as in Boomsma and van Loon 1982; this study) or even indirectly (as in Davidson 1977).

Reproductive output

Determining production of alate sexuals is a key estimate of colony productivity in the social insects (Wilson 1971, Hölldobler and Wilson 1990), but it is difficult and laborious to obtain properly, particularly in species forming populous colonies (Baroni-Urbani et al. 1978). There were four problems associated with the estimate in this study. First, I did not measure the production of new workers. New workers represent an investment in growth, and colonies may allocate different proportions of excess energy into growth as well as reproduction (Brian 1965). Second, I measured reproductive output along forest edges and in grazed meadows in 1991, but measured it in overgrazed meadows in 1992. Ideally, I should have examined the output in each habitat in the same year to eliminate potentially confounding effects of different years. Third, I determined biomass by using the mean fresh masses of samples of males and females. A better method would have been to measure the fresh mass of sexuals from each colony because there is probably a tradeoff between the number of sexuals produced within a colony and the mean size of sexuals. Fourth, I estimated colony sizes by measuring the area of the base of the mound. A more direct but impractical method would have been to count all the ants in each colony. Together these shortcomings probably accounted for some of the variation in alate production. However, the general patterns among habitats and between colonies fed and not fed were clear despite the variation. In part, this clarity resulted because I compensated for the shortcomings by working with large sample sizes and controlling for nest area.

I supplemented the diets of treatment colonies with both tuna and honey to be certain they were fed *ad libitum*. Tuna was probably the key to increasing alate production, because a protein source is essential for brood production. However, honey also may have played a role because it provided fuel for worker activity. The use of honey by workers would have made more tuna and natural prey available for alate production. Laboratory experiments have been performed to distinguish between the relative importance of protein and carbohydrate sources in brood production (Porter 1989). Porter's study demonstrated that a sugar source, though not essential, is important for brood production.

Because the density of *F. podzolica* colonies was considerably greater along forest edges, intraspecific competition for food was potentially highest in this habitat. Nonetheless, colonies appeared to be more food limited in overgrazed meadows because alate production was greatest along forest edges and lowest in overgrazed meadows. Moreover, there was no difference in reproductive output between fed colonies in overgrazed meadows and unfed ones along forest edges. My estimate of production of sexuals was not biased among habitats by using the mean fresh mass of samples of males and females, because mass and headwidths are highly correlated in ants (Savolainen 1990), and there were no differences among habitats in headwidths for both males and females. Headwidths and fresh masses were greater in females than males, however, as is typical in ants (Hölldobler and Wilson 1990).

Mixed results have been the outcome of experimental studies that manipulated food supply by feeding ant colonies or adding or removing neighbouring colonies believed to be competing exploitatively for food, and then evaluated the treatment effect on alate production or colony density. In general, experiments with various species of desert harvester ants have produced no short-term treatment effects on colony density (MacKay 1981, Davidson et al. 1985) or alate production (MacKay 1981, Munger 1992). The exceptions are the works of Davidson et al. (1984), which led to significant treatment effects on density of colonies of *Pheidole* spp., and Ryti and Case (1988), which led to marginally significant treatment effects on alate production in *Messor (= Veromessor) pergandei* after three years. In contrast, experiments with various species of temperate grassland ants have produced clear, short-term treatment effects on alate production (Pontin 1961, 1969, this study) or colony density (Yasuno 1965). Similarly, Backus and Herbers (1992) found an increase in total reproductive investment on food-supplemented plots by colonies of the forest ant, *Leptothorax longispinosus*. However, their results were less pronounced, perhaps because the quantity of food provided was insufficient.

I postulate that results of experimental studies of desert harvester ants differ from those of temperate grassland and forest ants in part because of differences in the species' ability to hoard food. Harvester ants along with honey-pot and carnivorous ants are the three groups known to store food in quantity (MacKay and MacKay 1984, Vander Wall 1990). Harvester ants store seeds of grasses and forbs in nest chambers (MacKay and MacKay 1984); honey-pot ants have a special caste of repletes that hold nectar and honeydew in greatly enlarged gasters and serve as living storage containers (McCook 1882, Conway 1977); and carnivorous ants of the subfamily Ponerinae sting invertebrate prey and store them in a living but dormant state for weeks or months (Maschwitz et al. 1979, Hölldobler 1982). The hoarding ability of these ants may moderate or militate against changes in colony density or alate production due to a shortage of food in the short-term. In contrast, temperate grassland or forest ants do not directly store food in any special way, probably because their dead prey do not keep well. At best, they may assimilate lipids and proteins and store them as body tissue (Stradling 1978, personal observation). As a result, they may be more sensitive to fluctuations in food supply and respond to these fluctuations even within one reproductive cycle.

E. Summary

1. In Elk Island National Park, Alberta, Canada, I studied the role of food supply in structuring a population of the ant *Formica podzolica* by examining the association between habitats differing in natural food levels and abundance, distribution and alate production of colonies. In addition, I compared alate production of colonies supplemented and not supplemented with food.

2. Nest densities and reproductive output of colonies were greatest along forest edges, intermediate in grazed meadows and lowest in overgrazed meadows. These patterns among habitats were associated positively with natural food levels in April and May, but not June 1992.

3. Colonies were dispersed uniformly on plots along forest edges, but dispersed either uniformly or randomly on plots in grazed and overgrazed meadows.

4. Females were larger than males, but size of neither males nor females differed significantly among habitats. Alate production was correlated positively with colony size.

5. Fed colonies in overgrazed meadows (the poorest habitat) produced significantly more sexuals within one reproductive cycle than those of unfed, control colonies, but not so compared to unfed colonies along forest edges (the best habitat).

6. I compared my experimental results with those of related studies of ants. In contrast to species that store food, I concluded that species storing relatively little food are more sensitive to changes in food supply, and respond to food addition in the short-term, even within one reproductive cycle.

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Table 2.1. Dispersion of *F. podzolica* nests on 15 study plots across habitats. R is an index of dispersion (Clark and Evans 1954). An R of 0 indicates perfect aggregation, an R of 1, random dispersion, and an R of 2.1491, perfect hexagonal uniformity. Plots marked with an asterisk were surveyed in 1992. All other plots were surveyed in 1991.

Habitat	Plot	Plot area (m^2)	N nests	R	P	Dispersion pattern
Forest edge	1	20	29	1.33	0.0006	**Uniform**
	2	25	28	1.60	< 0.0002	**Uniform**
	3	24	27	1.50	< 0.0002	**Uniform**
	4	45	26	1.57	< 0.0002	**Uniform**
	5	51	80	2.03	< 0.0002	**Uniform**
Grazed meadow	1	1080	32	1.03	0.779	Random
	2	1050	45	0.92	0.285	Random
	3	323	36	0.98	0.826	Random
	4*	2400	30	1.28	0.003	**Uniform**
	5*	1024	26	1.17	0.089	Random
Overgrazed meadow	1	1650	28	1.19	0.055	Random
	2	4500	27	1.23	0.021	**Uniform**
	3	8100	30	1.16	0.095	Random
	4*	4800	28	1.21	0.033	**Uniform**
	5*	4800	24	1.24	0.023	**Uniform**

Table 2.2. Mean (± se) densities and nearest-neighbour distances of nests of *F. podzolica* across habitats and results of Kruskal-Wallis tests. I had five study plots in each habitat.

Habitat	Nest density (n/m^2)	Nearest-neighbour distance (m)
Forest edge	1.17 ± 0.17	0.78 ± 0.079
Grazed meadow	0.044 ± 0.017	3.27± 0.74
Overgrazed meadow	0.0075 ± 0.0024	7.90 ± 0.87
Statistic	H = 12.02, df = 2	H = 12.02, df = 2
P	= 0.0025	= 0.0025

Table 2.3. ANOVA of headwidths (mm) of males and females of *F. podzolica* from colonies across habitats. N is number of colonies sampled. I measured the headwidths of 30 sexuals from each colony.

	Habitat		
Sex	Forest edge	Grazed meadow	Overgrazed meadow
Males			
$\bar{x}$ ± se	1.70 ± 0.0061	1.69 ± 0.0067	1.68 ± 0.0088
n	31	30	16
Females			
$\bar{x}$ ± se	1.85 ± 0.0061	1.85 ± 0.0071	1.84 ± 0.011
n	31	30	10

Source of variation	df	MS	F	P
Sex	1	0.935272	733.30	< 0.0001
Habitat	2	0.001098	0.86	0.43
Sex x Habitat	2	0.001020	0.80	0.45
Error	142	0.001275		

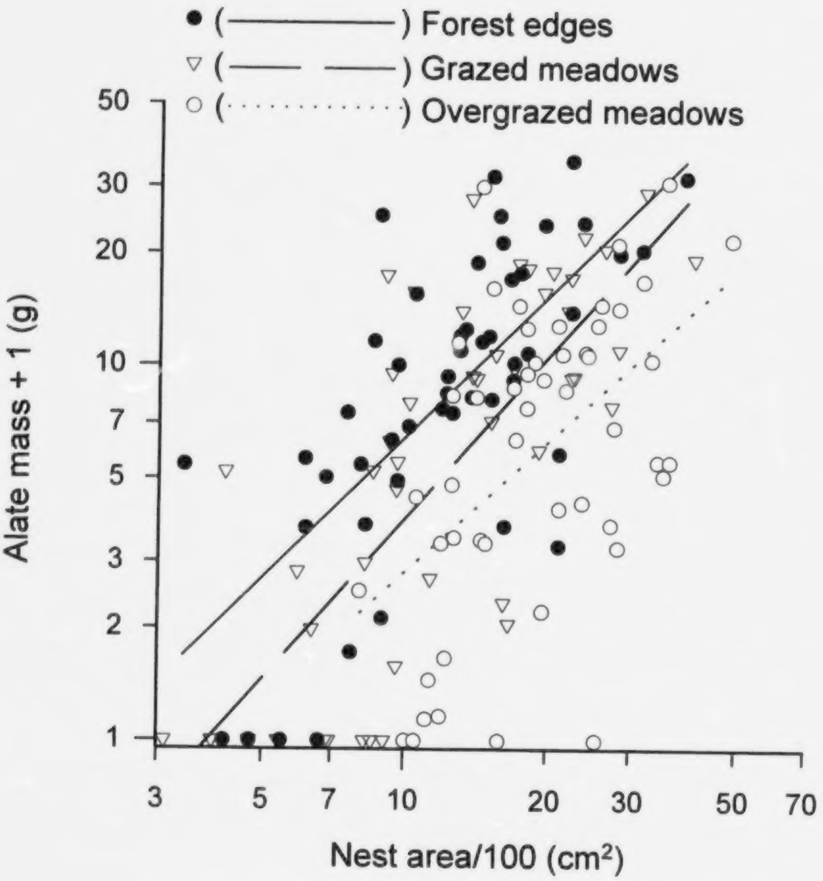

Fig. 2.1. Production of alates by colonies of *F. podzolica* located across habitats. Each regression between log mass of alates + 1 and log area of base of nest was significant (forest edge: $Y = 1.25X - 2.93$, $r^2 = 0.49$, $F_{1,48} = 45.85$, $P < 0.0001$; grazed meadow: $Y = 1.42X - 3.68$, $r^2 = 0.52$, $F_{1,48} = 51.61$, $P < 0.0001$; overgrazed meadow: $Y = 1.17X - 3.06$, $r^2 = 0.26$, $F_{1,48} = 17.09$, $P < 0.0001$). Regression coefficients did not differ significantly ($F_{2,144} = 0.37$, $P = 0.69$). Production differed significantly among habitats ($F_{2,146} = 16.19$, $P < 0.0001$).

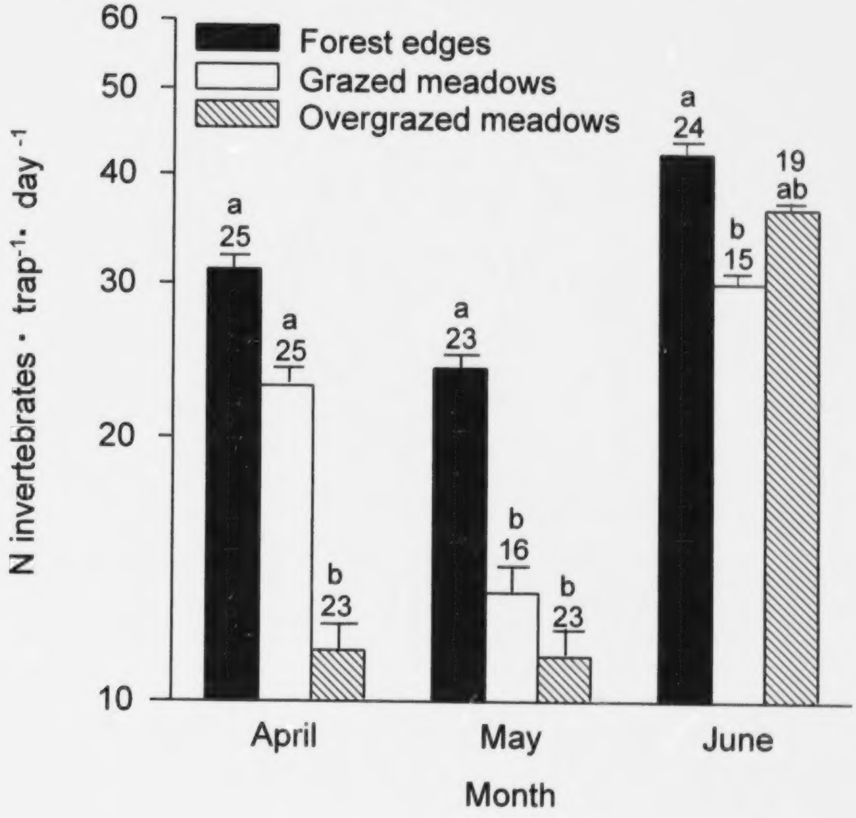

Fig. 2.2. Log number of invertebrates per pitfall trap per day in traps in different habitats in April, May and June, 1992. Error bars show one standard error above the mean. In two-way ANOVA, $F_{Habitat} = 51.98$, df = 2, 184, $P < 0.0001$; $F_{Month} = 69.07$, df = 2, 184, $P < 0.0001$; $F_{Habitat\ x\ Month} = 9.49$, df = 4, 184, $P < 0.0001$. Sample sizes are indicated by numbers above error bars. Shared letters within months designate means that did not differ significantly (Tukey $P > 0.05$).

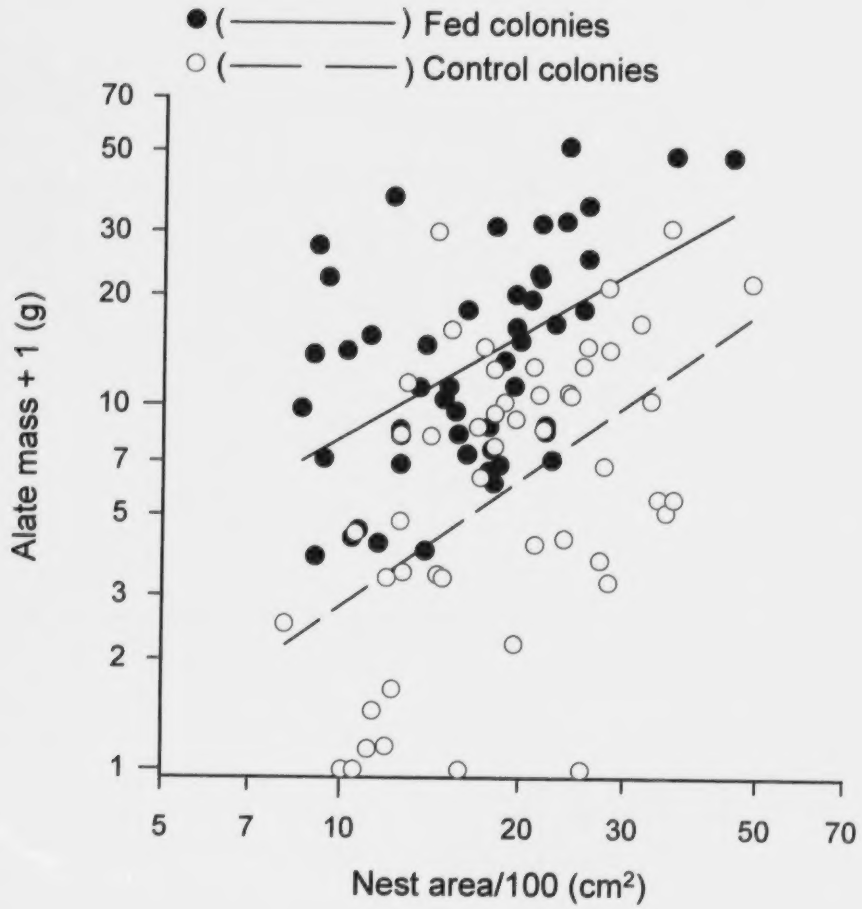

Fig. 2.3. Production of alates of *F. podzolica* by control and fed colonies. Both regressions between log mass of alates + 1 and log area of base of nest were significant (Control: $Y = 1.14X - 2.98$, $r^2 = 0.25$, $F_{1,48} = 16.18$, $P < 0.0002$; Fed: $Y = 0.94X - 1.91$, $r^2 = 0.26$, $F_{1,48} = 16.67$, $P < 0.0002$). Regression coefficients did not differ significantly ($F_{1,96} = 0.30$, $P = 0.58$). Production by fed colonies was significantly greater than that of control colonies ($F_{1,97} = 41.86$, $P < 0.0001$).

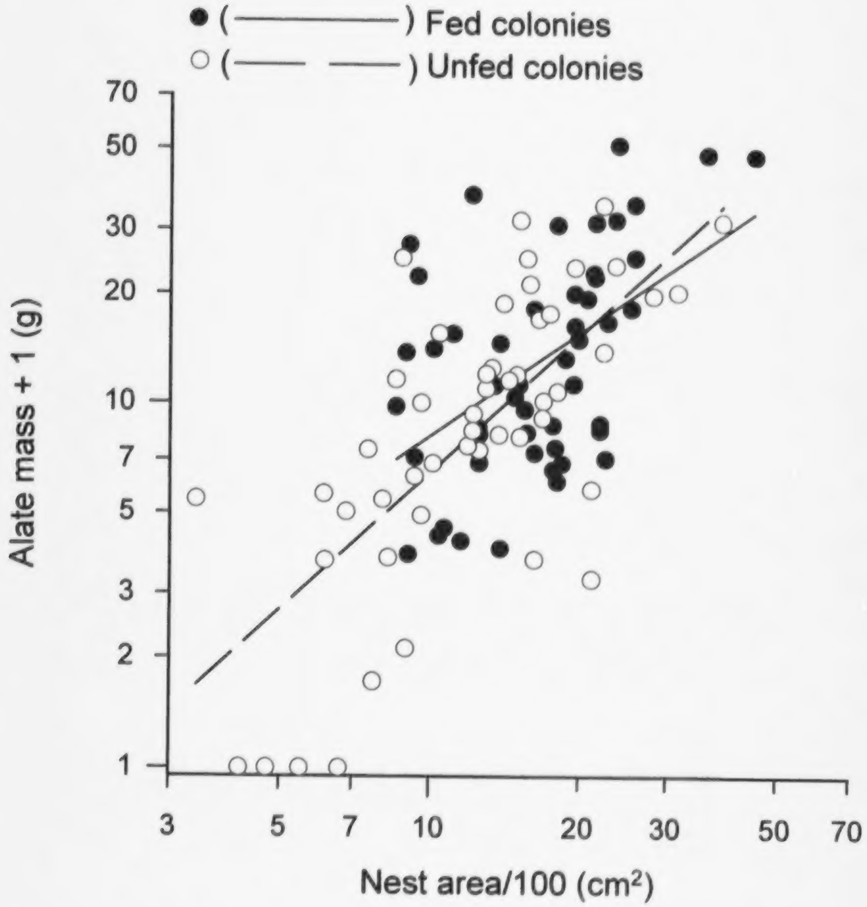

Fig. 2.4. Production of alates of *F. podzolica* by fed colonies in overgrazed meadows and unfed ones along forest edges. Both regressions between log mass of alates + 1 and log area of base of nest were significant (Fed: Y = 0.94X - 1.91, r^2 = 0.26, $F_{1,48}$ = 16.67, $P < 0.0002$; Forest edge: Y = 1.25X - 2.93, r^2 = 0.49, $F_{1,48}$ = 45.85, $P < 0.0001$). Regression coefficients ($F_{1,96}$ = 1.04, P = 0.31) and production by fed and unfed colonies ($F_{1,97}$ = 0.69, P = 0.41) did not differ significantly.

CHAPTER 3

SEX INVESTMENT IN A SOCIAL INSECT: THE PROXIMATE ROLE OF FOOD

A. Introduction

In eusocial Hymenoptera, males and females develop from unfertilized and fertilized eggs, respectively, a mode of sex determination termed haplodiploidy (Crozier 1971, Slobodchikoff and Daly 1971). Trivers and Hare (1976), by combining theories of kin selection (Hamilton 1964) and sex ratio (Fisher 1958), explained that haplodiploidy creates relatedness asymmetries among colony members, and these asymmetries lead to parent-offsping conflict over sex investment. Specifically, workers are more closely related to their sisters ($r = 3/4$) than their brothers ($r = 1/4$), since sisters share on average half the genes they receive from their mother and all genes they receive from their father, but share with their brothers only half the genes from their mother. Furthermore, the mother (i.e., queen) is symmetrically related ($r = 1/2$) to both her male and female offspring as in diploid organisms. Consequently, workers strive for a 3:1 female-biased ratio of sex allocation, and queens strive for a 1:1 ratio. Refinements of this hypothesis confirm the same general prediction of female-bias under worker control, but the bias is not necessarily 3:1(Craig 1980, Uyenoyama and Bengtsson 1981, Pamilo 1982, Matessi and Eshel 1992).

This framework has stimulated many empirical studies of sex investment in hymenopterans, and the balance of evidence supports predictions of a genetic relatedness hypothesis (reviews by Nonacs 1986a, Boomsma 1989). However, the variation in allocation ratios both within and among species is great, and remains mostly unexplained (Alexander and Sherman 1977, Nonacs 1986a, Herbers 1990). Many factors influence sex investment including egg laying by workers, polygyny, local mate competition, inbreeding and food supply (Alexander and Sherman 1977, Nonacs 1986a, Bourke 1988, Herbers 1990). The latter is important in part because food affects whether a fertilized egg becomes a sterile worker or a reproductive gyne (Hölldobler and Wilson 1990).

Results of several studies provide circumstantial evidence for a link between food supply and sex investment in ants. Pontin (1961) reported an increase in female production when neighbouring colonies of a competing species were removed. The manipulation presumably increased the amount of resources available to focal colonies. Similarly, several investigators have detected greater female-bias in optimal compared to suboptimal habitats that differed in estimated levels of resources (Brian 1979; Boomsma et al. 1982; Rosengren and Pamilo 1986). Finally, Herbers (1990) compared a population of *Leptothorax longispinosus* in New York and Vermont over seven years and described a consistent site difference in allocation ratios. The pattern indicated an association between sex investment and a consistent ecological factor.

In an experimental study, Backus and Herbers (1992) tested whether this factor was food supply by adding protein both to the diet of laboratory colonies and to study plots in Vermont. They found an increase in total alate production due to an increase in male, but not female production, and argued that food limitation cannot be responsible for the observed population differences in sex allocation. The amount of supplemented diet may have been insufficient, however, making their conclusion premature. Therefore, the proximate role of food in determining sex allocation remains unclear and warrants further experimental studies.

In this chapter, I examine sex investment in the ant, *Formica podzolica*. I have four objectives: (1) to compare abundance, sex ratio and sex investment of colonies and size of workers across habitats differing in natural food abundance. I made these comparisons to determine whether patterns in these variables were associated with food supply; (2) to compare size of workers in colonies producing all male, all female or both male and female sexuals. I made this comparison to test for an indirect link between food supply and sex investment. Under a food hypothesis, one expects worker size to be positively correlated with food intake (Hölldobler and Wilson 1990). In turn, caste determination should be related to food intake with well-fed colonies producing more female sexuals on average than poorly-fed colonies (Nonacs 1986a,b); (3) to assess experimentally whether food supply affects sex allocation within one reproductive cycle; and (4) to compare allocation of monogynous (i.e., one queen per nest) and polygynous (i.e., many queens per nest) colonies. Theory predicts that under worker control, investment ratios should be more female-biased in monogynous colonies than in polygynous colonies because increasing queen number reduces the asymmetry in relatedness between sisters and brothers (Trivers and Hare 1976).

B. *Study area*

I conducted field work in Elk Island National Park (53° 37' N, 112° 58' W), Alberta, Canada, from 1990 to 1993. The Park covers 195 km^2, ranges in elevation from 710 to 755 m above sea level, and represents the transition between the boreal mixed-wood forest of northern Alberta and the grasslands of the south. Most of the Park is composed of trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) forests, and the remainder is wetlands, boreal mixed-wood forests, sedge meadows, shrublands and grasslands.

I established study sites along edges of the aspen-poplar forests and in grazed and overgrazed meadows. Grazing pressure by ungulates, especially bison (*Bison bison*), was similar along forest edges and in grazed meadows. However, it was clearly greater in overgrazed meadows where large herds of bison fed daily. On all study plots, the soil was either an orthic or dark gray luvisol (Crown 1977), and the vegetation was mainly grasses and a few shrubs . Further details on the study sites are provided in Chapter 1.

Formica podzolica is widely distributed in North America, and is most abundant at higher elevations and in northern regions (Francoeur 1973). It is the numerically dominant formicine in Elk Island National Park, and is a medium-sized, black ant that nests primarily in soil. Colonies form conspicuous earthen mounds, the largest of which exceed 2 m in diameter. I estimate that colonies producing sexual offspring typically contain between 5 000 and 40 000 workers, and the largest ones exceed 100 000 workers. Workers tend homopterans for honeydew, and they scavenge and prey on many species of invertebrates from March to October. The sexuals leave the nests from late July to early September to mate, and thereafter, males die, and females try to start new colonies.

C. Materials and methods

I used three methods to study production of sexuals in *F. podzolica*. First, I surveyed 15 plots along forest edges and in grazed and overgrazed meadows to compare nest density and gross investment in sexuals within and across habitats. In each survey, I measured the length and width of each nest, and noted whether the nest had sexuals. If so, I did a partial excavation and estimated the proportion of males and females. Because the sexual brood of most colonies was unisexual (see Results), I classified them as either male or female. I conducted the surveys in 1991 and 1992, before the first nuptial flight of the year.

Second, I excavated 100 nests of *F. podzolica*, 50 each along forest edges and in grazed meadows, to compare sex allocation within and between habitats more accurately than was possible with surveys. I selected colonies haphazardly, without prior knowledge of their investment in sexuals. I excavated the nests in 1991 before the first nuptial flight of the year. I counted all sexuals in each colony and determined total reproductive output (in grams) by the equation:

$$(\text{Number of males} \times 0.0182) + (\text{Number of females} \times 0.0314) \qquad (1)$$

and investment ratio, R, by the equation:

$$(\text{Number of males} \times 0.0182) \,/\, \text{equation } (1) \qquad (2)$$

where the values 0.0182 and 0.0314 are the mean fresh masses in grams of males and females, respectively (Chapter 2). An R of 0.50 indicates equal investment in each sex, and an $R < 0.50$ indicates female bias.

Third, I did a food-addition experiment in 1992 in overgrazed meadows to determine whether food affected sex investment in *F. podzolica* within one reproductive cycle. I conducted the experiment in overgrazed meadows since they were poor in natural supply of invertebrates (Chapter 2). In March 1992, I selected 50 control and 50 treatment colonies scattered throughout overgrazed meadows, and placed a small rock labelled with a unique mark on top of the mound to identify the nest. I fed each treatment colony 50 times from April to July by pouring undiluted liquid honey on the rock placed on each colony, and scattering tuna in small pieces on and around the mound. Overall, I provided about 4 L of honey and 34 kg of tuna. Although workers of neighbouring colonies of *F. podzolica*, and *Myrmica* spp. consumed some honey and brought small amounts of tuna to their nests, treatment colonies consumed most of the food. I excavated all 100 colonies in July 1992 before the first nuptial flight of the year. I counted the sexuals and determined total reproductive output and sex investment in the same manner described above.

In addition, I measured the headwidth of workers from 178 colonies along forest edges and in grazed and overgrazed meadows to compare size across habitats and in colonies producing all-male, both male and female and all-female sexuals. For each colony sampled, I measured the headwidth of 30 workers, and noted whether the sexual offspring was all-male, both male and female or all-female. I sampled in July of 1991 or July of 1992 before the first nuptial flight of the season.

I report descriptive statistics as means ± one standard error, and used standard inferential statistics to analyze data when variances were homogeneous by the F_{MAX} test (Sokal and Rohlf 1981). Before parametric analyses of percentages or proportions, I used the arcsine transformation. I tested the null hypotheses of no difference in density among habitats with a Kruskal-Wallis test, and located the significant differences with a Tukey-type multiple comparison test (Zar 1981). Using ANOVA, I tested the null hypotheses of no differences in percentage of nests with sexuals or sex ratio across habitats. With two-way ANOVAs and Tukey multiple comparison tests, I tested the null hypotheses of no difference in worker headwidths from colonies across habitats and in colonies producing all-male, both male and female or all-female sexuals, and no difference in sex investment from colonies across gyny (i.e., colonies differing in number of queens). To test the null hypothesis of no association between percentage male mass and total mass for each habitat or treatment, I used linear regression. Finally, I used log-likelihood analyses to test the null hypotheses of no association between colonies producing all-male, both male and female or all-female sexuals and colonies located along forest edges or in grazed meadows, and no association between colonies producing all-male, both male and female or all-female sexuals and treatment using log-likelihood tests.

D. Results

Patterns across habitats

The percentage of *F. podzolica* nests producing sexuals did not differ significantly across habitats on study plots. However, nest density was different across habitats, and was highest along forest edges and lowest in overgrazed meadows (Tables 3.1, 3.2). The only significant pairwise comparison of nest density was between forest edge and overgrazed meadows ($q = 4.90$, $P < 0.005$).

Headwidth of workers differed significantly both across habitats and across colonies that produced all-male, both male and female or all-female sexuals (Fig. 3.1). Headwidths were greatest in colonies located along forest edges and smallest in those located in overgrazed meadows. Likewise, they were greatest in colonies producing all-female sexuals and smallest in those producing all-male sexuals. There was no interaction between habitat and the sex of the colony (Fig. 3.1). In contrast to those of workers, headwidths of neither males nor females differed significantly across habitats (Chapter 2).

On average, population sex ratios were male-biased on study plots in each habitat. They were least biased along forest edges and most biased in overgrazed meadows, but the differences across habitats were not significant (Tables 3.1, 3.2). Similarly, complete excavations of colonies revealed a male bias in numerical and investment ratios of populations across habitats. Colonies were least biased along forest edges and more biased in grazed meadows. In addition, they were most biased in overgrazed meadows, but unlike colonies along forest edges and in grazed meadows, colonies in this habitat were excavated in 1992 (Table 3.3).

The sexual offspring of individual colonies were often either all-male or all-female. This pattern was most pronounced in the meadows, but the association between colonies located along forest edges and in grazed meadows and sex of colonies was not significant (Figs. 3.2, 3.3). In addition, there was no significant relationship between percent investment in males and total production of sexuals in each habitat (Fig. 3.2). Total production of sexuals and mound volume are correlated (Chapter 2), and, in turn, mound volume and number of workers are correlated (Savolainen and Deslippe submitted ms). Therefore, there was no clear relationship between percent investment in males and colony size.

Food-addition experiment

Sex investment of colonies was greatly affected by a supplemented diet. The population investment ratio was female-biased (R = 0.36) and male-biased (R = 0.62) for fed and unfed, control colonies, respectively (Table 3.3). The association between treatments and sex of colonies was significant, and although an equal number of fed and control colonies produced all-female brood, they produced a substantially different proportion of all-male and mixed-sex broods (Figs. 3.2, 3.3). In contrast to unfed colonies in each habitat, there was a marginally significant correlation between percent male mass and total mass of sexuals, but the explained variation was only 8% (Fig. 3.2).

Monogynous and polygynous colonies

Investment ratios were more male-biased in polygynous colonies than in either monogynous colonies or colonies with an unknown number of queens. The association between gyny and treatment was not significant both between colonies located along forest edges and in grazed meadows and between fed and unfed colonies (Fig. 3.4). Across levels of gyny, however, unfed colonies in each habitat produced fewer females than fed ones on average (Fig. 3.4).

E. Discussion

In this chapter, I examined the role of food supply in affecting sex investment in *F. podzolica*. I compared measures of productivity and investment across habitats, and compared sex investment of monogynous and polygynous colonies. In addition, I conducted a food-addition experiment in a suboptimal habitat. Results show that food supply has a major influence both on abundance, distribution and reproductive productivity of colonies (see also Chapter 2), and in determining sex allocation. Most importantly, the study provides the first experimental evidence that food plays a key proximate role in determining sex investment in field populations.

Across habitats, although percent of nests producing sexuals did not differ, there were consistent differences in nest density, worker headwidths, sex ratio and sex allocation. In addition, total production of sexuals differed significantly across habitats, and was highest along forest edges and lower in grazed meadows. In addition, it was lowest in overgrazed meadows, although colonies in this habitat were excavated in a different year than those located along forest edges and in grazed meadows (Chapter 2). These differences across habitats were positively associated with natural food supply, because food resources were greater along forest edges than in meadows (Chapter 2). The results indicate a strong link between food and reproductive parameters, a finding consistent with previous investigations (Brian 1979, 1989, Boomsma et al. 1982, Porter 1989, Backus and Herbers 1992).

The association between worker headwidth and sex of the sexual offspring produced by a colony provided indirect evidence for a link between food supply and sex investment. Under a food hypothesis, within limits one expects worker size to be positively correlated with food intake, because final adult size is largely determined by the quantity or quality of food consumed at the larval stage (Hölldobler and Wilson 1990). In turn, caste determination should be related to food intake with well-fed colonies producing female sexuals and poorly-fed colonies producing males (Nonacs 1986a,b). As a result, an association between worker size and sex of the sexual offspring produced is consistent with a food hypothesis, and this prediction was indeed realized in this study. In contrast to those of workers, headwidths of male and female sexuals did not differ with colony sex (Chapter 2), suggesting colonies tend to reduce number but not size of sexual offspring under food limitation.

The associations between reproductive parameters and habitats links these parameters to food supply, since resources differed significantly across habitats (Chapter 2). However, the cause of the associations may instead be another factor also varying consistently across habitats. My experimental test, therefore, provided more direct evidence for the importance of resources. Not only did fed colonies produce more sexuals than unfed colonies (Chapter 2), but they also invested more in females than males. Interestingly, this shift in sex investment was effected after supplemental feeding within only one reproductive cycle.

I supplemented the diets of treatment colonies with large quantities of both tuna and honey to be certain they were fed *ad libitum*. This supplementation may have altered not only the absolute amount of food, but also the proportion of protein and carbohydrates. Further study is needed to learn the importance of altering the protein to carbohydrate ratio of the diet. I suspect, however, that tuna was probably the key to increasing alate production, because a protein source is essential for brood production. The main role of honey may have been to provide fuel for worker activity. Laboratory experiments have been performed to distinguish between the relative importance of protein and carbohydrate sources in brood production (Porter

1989). Porter's study demonstrated that a sugar source, though not essential, is important for brood production.

Theoretical predictions of sex-allocation ratios apply in a given species to the population and not to individual colonies. Therefore, colonies producing only either males or females are not necessarily acting against the inclusive fitness of their workers (Taylor and Sauer 1980). In fact, individual colonies of most ants including *F. podzolica* tend to produce predominantly one sex or the other in any given year (Pamilo and Rosengren 1983, Nonacs 1986a, Herbers 1990). The only obvious exception presently known is provided by *Tetramorium caespitum* (Brian 1979). In general, this phenomenon of specialization is poorly understood. However, Taylor (1981), Grafen (1986) and Boomsma and Grafen (1990, 1991) have modelled certain situations where active selection for different sex ratios can occur at the level of separate colonies. For example, Boomsma and Grafen (1990, 1991) argue that colonies should usually produce predominantly one sex when relatedness asymmetry is variable among colonies due to multiple mating, worker reproduction and polygyny. Besides evolutionary considerations, the input of resources apparently serves as a proximate cue to the colony, because fed colonies in this study produced fewer all-male and more mixed-sex brood than did unfed colonies.

Under worker control, investment ratio should be 3:1 in monogynous colonies due to relatedness asymmetries, and should approach 1:1 in polygynous colonies because increasing queen number reduces the asymmetry in relatedness between sisters and brothers (Trivers and Hare 1976). Therefore, in facultatively polygynous species like *F. podzolica* (Chapter 5), the population sex ratio at equilibrium should lie between these extremes, a prediction confirmed in fed but not unfed colonies of this study. Although the number of known polygynous colonies were small, they were always more male-biased than known monogynous colonies. Similar results have been reported by others in comparisons both across and within species of ants (reviewed by Nonacs 1986a). Most colonies that I categorized as "unknown" undoubtedly contained queens; I simply did not find them. Whether I located queens was largely dependent on prevailing conditions. For example, queens were usually found when I excavated colonies on days following a cool or rainy period, as they were near the nest surface. In contrast, queens were rarely found when I excavated colonies following several warm, dry days, as they retreated deeply into the nest.

Because food supply has an important proximate influence on sex investment, it may account for part, perhaps much, of the great variability in sex investment typical in social Hymenoptera. At the ecological scale, further study is needed to determine how food supply and other factors affect the conflict over sex investment between queens and workers. Potential mechanisms include the queen controlling release of sperm from her spermatheca, or workers biasing the sex ratio by destroying or underfeeding males and channelling extra resources to females.

F. Summary

1. In eusocial Hymenoptera, relatedness asymmetries lead to conflict between parents and offspring over sex investment; workers strive for a 3:1 female-biased allocation ratio, and queens strive for a 1:1 ratio. Many studies support this genetic relatedness hypothesis, but ratios vary greatly in in natural populations, and the variation remains mostly unexplained.

2. Part of the variation may be due to variation in food resources. In this chapter, I examined the proximate role of food in determining sex investment of the ant *Formica podzolica.* I compared reproductive parameters of colonies and populations across habitats varying in natural food abundance, and compared sex allocation of fed and unfed colonies.

3. Nest density, worker size and sex allocation were all greatest along forest edges, intermediate in grazed meadows and lowest in overgrazed meadows. These patterns among habitats were associated with natural food levels.

4. There was a strong tendency for individual colonies to produce either all-male or all-female sexuals. Worker size was greatest in colonies producing all-females and smallest in those producing all-males.

5. Sex investment was greatly affected by a supplemented diet. The population investment ratio was female-biased ($R = 0.36$) and male-biased ($R = 0.62$) for fed and unfed, control colonies, respectively.

6. Investment ratios were more male-biased in polygynous colonies than in monogynous colonies as predicted by a genetic relatedness hypothesis.

7. These results demonstrate that food supply has an important proximate influence on sex investment. Potential mechanisms include the queen controlling release of sperm from her spermatheca, or workers biasing the sex ratio by destroying or underfeeding males and channelling extra resources to females.

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Table 3.1. Number of nests, nest density, percent of nests with sexuals and sex ratio of *F. podzolica* on 15 study plots across habitats. Plots marked with an asterisk were surveyed in 1992. All other plots were surveyed in 1991.

Habitat	Plot	N nests	Nest density (n/m^2)	% nests with sexuals	Sex ratio (M/F)
Forest edge	1	29	1.45	75.9	2.14
	2	28	1.12	54.1	0.60
	3	27	1.13	70.4	0.90
	4	26	0.58	65.4	0.89
	5	80	1.57	60.0	1.18
Grazed meadow	1	32	0.030	71.9	1.09
	2	45	0.043	77.8	0.94
	3	36	0.11	58.3	1.63
	4*	30	0.013	40.0	0.50
	5*	26	0.025	65.4	1.83
Overgrazed meadow	1	28	0.017	32.1	3.50
	2	27	0.0060	59.3	1.29
	3	30	0.0037	50.0	1.50
	4*	28	0.0058	67.9	2.80
	5*	24	0.0050	75.0	1.57

Table 3.2. Means (± se) of nest density, percent of nests with sexuals and sex ratio of *F. podzolica* and results of statistical tests of data presented in Table 3.1. I surveyed five study plots in each habitat.

Habitat	Nest density (n/m^2)	% with sexuals	Sex ratio (M/F)
Forest edge	1.17 ± 0.17	65.2 ± 3.82	1.14 ± 0.27
Grazed meadow	0.044 ± 0.017	62.7 ± 6.54	1.20 ± 0.24
Overgrazed meadow	0.0075 ± 0.0024	56.9 ± 7.47	2.13 ± 0.43
Statistic	H = 12.02, df = 2	$F_{2,14} = 0.47$	$F_{2,14} = 2.94$
P	= 0.0025	= 0.64	= 0.091

Table 3.3. Production of sexuals by colonies of *F. podzolica* across habitats and between fed and unfed colonies based on complete excavations of colonies. I include only colonies that produced sexuals. Note sex investment was female-biased in fed colonies, and investments were male-biased in unfed colonies.

	Habitat			
Variable	Forest edge	Grazed meadow	Overgrazed meadow	Overgrazed meadow
Sampling year	1991	1991	1992	1992
Food added	No	No	No	Yes
N colonies	46	38	46	50
N males	15545	12439	12633	15083
N females	7786	4920	4587	15867
Mass males (g)	282.9	226.4	229.9	274.5
Mass females (g)	244.5	154.5	144.0	498.2
Sex ratio (M/F)	2.00	2.53	2.75	0.95
Investment ratio (R)	0.54	0.59	0.62	0.36

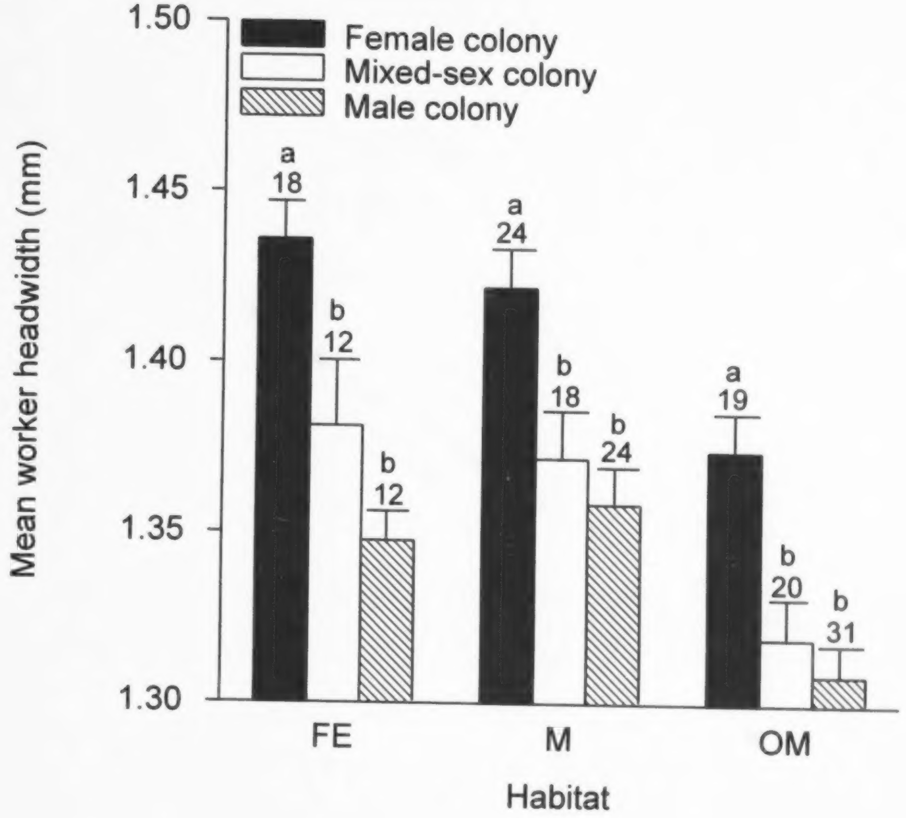

Fig. 3.1. Mean headwidth of workers from colonies producing sexuals that were all-female, both male and female or all-male. I sampled along forest edges (FE), in grazed meadows (M) and in overgrazed meadows (OM). In two-way ANOVA, $F_{Habitat} = 21.04$, df = 2, 169, $P < 0.0001$; $F_{Colony\ sex} = 37.47$, df = 2, 169, $P < 0.0001$; $F_{Habitat\ X\ Colony\ sex} = 0.35$, df = 4, 169, $P = 0.85$. Sample sizes are indicated by numbers above error bars. Shared letters within habitats designate means that did not differ significantly (Tukey $P > 0.05$).

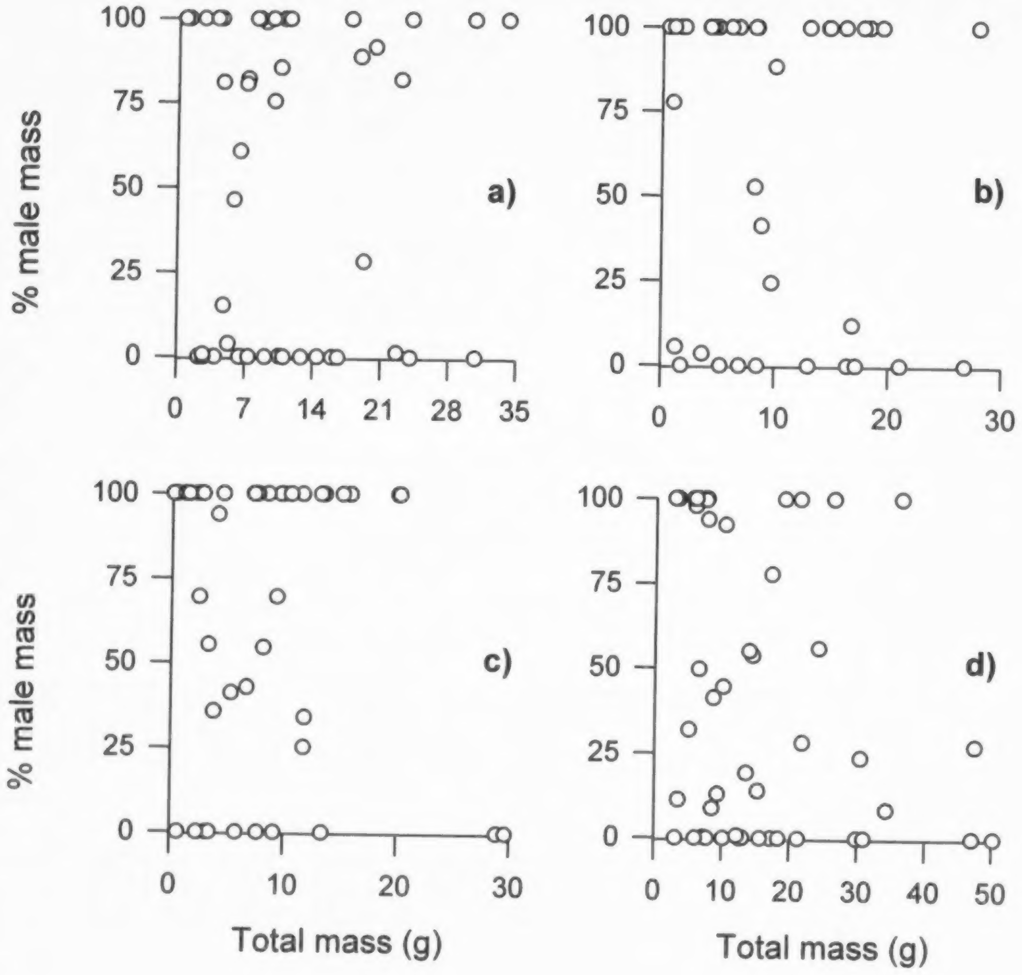

Fig. 3.2. Percent male mass versus total mass of sexuals for unfed colonies located (a) along forest edges, (b) in grazed meadows, and (c) in overgrazed meadows, and for fed colonies located (d) in overgrazed meadows. Colonies along forest edges and grazed meadows were excavated in 1991 and colonies in overgrazed meadows were excavted in 1992. The relationship was not significant for unfed colonies [(a) Y = 0.13X + 51.14, r^2 = 0.00, $F_{1, 44,}$ P = 0.87; (b) Y = -0.02X + 11.23, r^2 = 0.02, $F_{1, 36}$ = 0.57, P = 0.46; (c) Y = -0.01X + 8.69, r^2 = 0.00, $F_{1, 44}$ = 0.16, P = 0.69], but was marginally significant for fed colonies [(d) Y = -0.08X + 19.06, r^2 = 0.08, $F_{1, 48}$ = 4.40, P = 0.04].

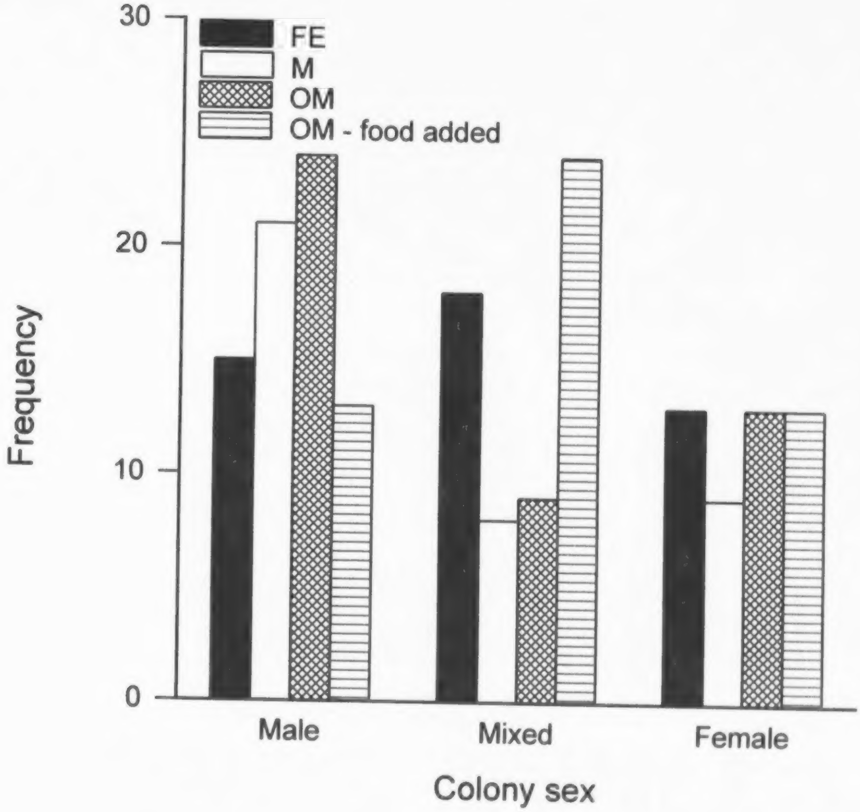

Fig. 3.3. Number of unfed colonies located along forest edges (FE), and in grazed (M) and overgrazed meadows (OM), and fed colonies in overgrazed meadows producing sexuals that were all-male, male and female or all-female. Colonies along forest edges and grazed meadows were excavated in 1991 and colonies in overgrazed meadows were excavated in 1992. The association between sex of the colony (i.e., all-male, male and female and all-female) and habitat (i.e., forest edge and grazed meadow) was not significant ($G_{adj} = 4.92$, df = 2, P = 0.09). However, the association between sex of the colony and treatment (food supplemented and control colonies in overgrazed meadows) was significant ($G_{adj} = 10.22$, df = 2, P = 0.006).

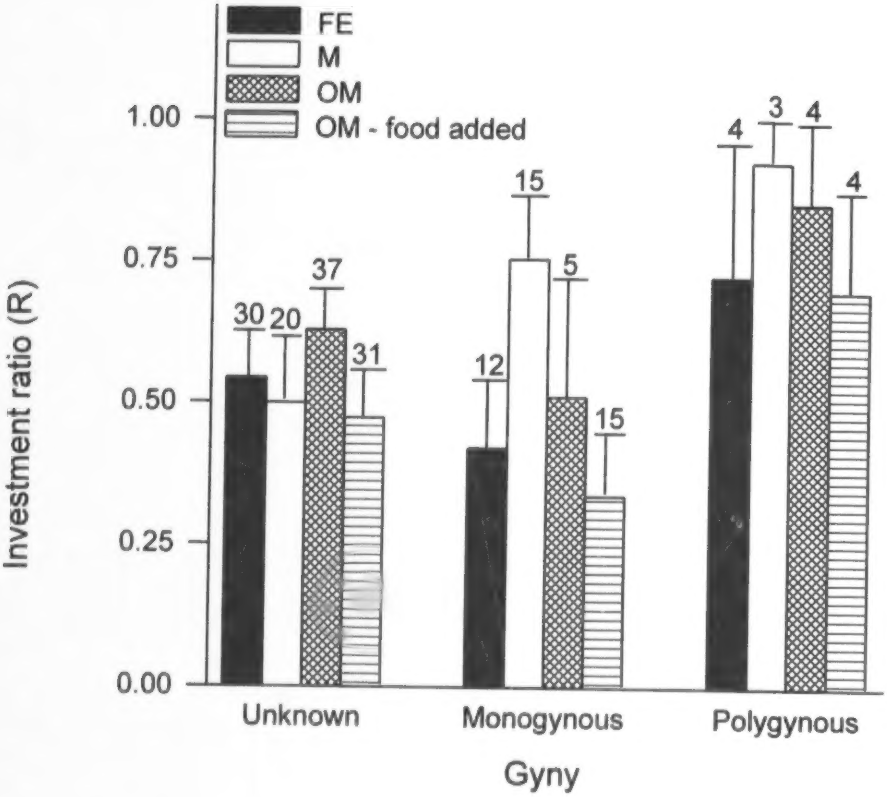

Fig. 3.4. As a function of nest gyny, mean (± se) investment ratio, R, of unfed colonies located along forest edges (FE), in grazed meadows (M) and in overgrazed meadows (OM), and fed colonies in overgrazed meadows. Investment ratios did not differ for colonies excavated in 1991 along forest edges and in overgrazed meadows (Gyny: $F_{2,78}$ = 1.16, P = 0.30; Habitat: $F_{1,78}$ = 1.70, P = 0.20; Gyny x Habitat: $F_{2,78}$ = 1.38, P = 0.26), and did not differ between food supplemented and control colonies excavated in 1992 in overgrazed meadows (Gyny: $F_{2,90}$ = 1.75, P = 0.18; Treatment: $F_{1,90}$ = 1.63, P = 0.21; Gyny x Treatment: $F_{2,90}$ = 0.012, P = 0.99).

CHAPTER 4

MECHANISMS OF COMPETITION IN A GUILD OF FORMICINE ANTS

A. Introduction

Spatial dispersion of a uniform or regular arrangement in plant and animal populations usually is interpreted as evidence for competition, as sessile individuals are assumed either to avoid others or to have previously eliminated neighbours (Goodall 1970, Yeaton and Cody 1976, Levings and Traniello 1981, Levings and Franks 1982). Although other processes like predation or microhabitat preferences of colonizing propagules can produce the pattern, the inference of competition is generally accepted in social insects, a group in which uniform spacing of colonies is common (Levings and Traniello 1981, Levings and Adams 1984, Johnson et al. 1987, Cushman et al. 1988). This acceptance is facilitated because competitive interactions among social insects are often easy to demonstrate (Wilson 1971, Hölldobler and Wilson 1990).

Not so clear, however, is the way in which competition produces regular spacing. Potential mechanisms include members of established colonies (1) killing or repelling founding queens, (2) eliminating neighbouring colonies, (3) killing foragers or inhibiting their foraging activities, and (4) competing exploitatively for a limited resource like food. To date, only Ryti and Case (1986, 1988a,b) have tried to distinguish experimentally among some of these and other possibilities. They found that resource competition and perhaps space preemption by established colonies account for the uniform dispersion of colonies in two species of desert ants.

In chapter 2, I showed that nests of the ant *Formica podzolica* were arranged uniformly, particularly along forest edges where food is more abundant than in meadows. Moreover, the nests are generally absent near established colonies of other *Formica* species (personal observation). In this chapter, I explore three mechanisms of intra- and interspecific competition that may account for the observations. I have three objectives: (1) to test whether established colonies prevent *F. podzolica* foundresses from starting new colonies near their nests, and compare the degree of space preemption by four species; (2) to test whether established colonies eliminate small colonies of *F. podzolica* transplanted near their nests, and compare the degree of interference across species; and (3) to test whether diffuse competition among established colonies of *F. podzolica* affects sexual production and sex-investment ratios.

B. *Study area*

I conducted field work in Elk Island National Park (53° 37' N, 112° 58' W), Alberta, Canada, from 1990 to 1993. The Park covers 195 km^2, ranges in elevation from 710 to 755 m above sea level, and represents the transition between the boreal mixed-wood forest of northern Alberta and the grasslands of the south. Most of the Park is composed of trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) forests, and the remainder is wetlands, boreal mixed-wood forests, sedge meadows, shrublands and grasslands. I conducted studies along the edges of the aspen-poplar forests where the vegetation was mainly grasses and a few shrubs, and the soil was either an orthic or dark gray luvisol (Crown 1977). Further details on the study sites are provided in Chapter 1.

Formicine ants are very common in the Park, and they rank from most to least abundant as follows: *F. podzolica* (host of all temporary social parasites and slave-makers), *F. dakotensis* (temporary parasite), *F. subnuda* (facultative slave-maker), *F. ulkei* (temporary parasite), *F. subintegra* (obligate slave-maker) and *Polyergus breviceps* (obligate slave-maker). In temporary parasites, newly fertilized queens penetrate host colonies and secure adoption. The original host queens are killed leading to production of only parasitic brood, and once the host workers die out, colonies consist entirely of parasitic queens and their offspring. In slave-makers, queens also penetrate host colonies and secure adoption. Unlike colonies of temporary parasites, however, both parasitic and host workers are normally present. This mix arises because armies of slave-making workers raid foreign nests, capture brood, and rear them as enslaved nestmates (Buschinger 1986, Hölldobler and Wilson 1990).

I examined mechanisms of competition between colonies of *F. podzolica* alone, and between colonies of *F. podzolica* and the parasites *F. dakotensis*, *F. subnuda* and *F. ulkei*. Workers of each of these species are medium-sized, tend homopterans for honeydew, and scavenge and prey on various invertebrates. Colonies nest in soil, forming conspicuous earthen or thatch mounds. Mating flights occur from late June to early September, and although *F. subnuda* is generally first to fly (personal observation), there is considerable overlap in timing of flights. The hosts and parasites are readily distinguished, because *F. podzolica* is a black ant whereas the parasites are red ants. I provide additional comparisons of these species in the results section.

C. Materials and methods

Characteristics of species

To compare foraging distances of workers across species, I measured the maximum foraging distances of workers from their colonies in June and July, 1992. I observed workers from each colony for up to an hour and measured the maximum distance from their nest. Three of the four species use recruitment trails while foraging, (i.e., foragers form trails leading from the nest), so the colony of worker origin was clear. It was not clear in *F. podzolica,* so I confirmed the colony of origin in this species by giving workers small chironomids and following the homing ants. I also made regular qualitative observations on activity levels, aggressiveness and recruitment ability on each species during daylight hours from May to September, 1990-93.

Foundation experiment

I conducted a colony founding experiment to determine whether established colonies prevent queens of *F. podzolica* from starting new colonies near their nests, and whether the degree of space preemption depends on the species of and distance to the nearest established colony. I used bison dung as the colonizing substrate in the experiment for it is readily used by founding queens. Dung piles were collected in Elk Island National Park and placed either far from (> 350 cm) or near (30 to 150 cm) established colonies of *F. podzolica*, *F. dakotensis*, *F. subnuda* and *F. ulkei.* I moved the piles in late July 1991-93, before the mating flight of *F. podzolica*, and searched them for queens in late August or early September of each year. For each replication, I used 20 piles about 20 cm in diameter, and arranged them in four rows of five. For each replication, I placed a pile in each row either 30, 60, 90, 120 or 150 cm from the established colony. These distances were well within the foraging radius of each species (see Results). A diagram of the experimental setup is shown in Fig. 4.1.

Transplant experiment

To determine whether interference competition affected survivorship of *F. podzolica* colonies, I relocated colonies and varied size of transplants, and species of and distance to the nearest established colony. Transplants were composed of either 1 queen and 50 workers or 1 queen and 1 500 workers. I relocated control colonies far (> 350 cm) from established formicine colonies, and relocated treatment colonies near (30 or 150 cm) established formicine colonies. As in the founding experiment, the neighbouring species were the formicines *F. podzolica*, *F. dakotensis*, *F. subnuda* and *F. ulkei*.

Transplants were subsets of larger colonies. I made them by partially excavating colonies in the field, and placed nest material, a reproductive queen and 50 or 1 500 workers in a plastic container. The container was rimmed with Teflon paint, Fluon™, to prevent escape of ants. I transplanted 150 colonies from June 16 to July 12, 1991. At each selected site, I loosened the soil with a shovel to a depth of about 50 cm, and buried a large tin can (with no top or bottom) halfway into the ground. I rimmed each can with Fluon, then dumped a colony in it. I removed the cans after 24 to 48 hours, and placed a ceramic tile (10 x 20 cm) over the newly constructed nest. I regularly checked some colonies to assess their fates, and examined all of them on August 26 and August 27, 1991, to determine whether they had survived.

Removal experiment

To determine whether diffuse competition affected productivity and sex investment of *F. podzolica* colonies, I conducted a neighbour-removal experiment in 1992 and 1993. I selected 32 colonies and randomly picked 16 of them as controls. To the other 16, I removed all conspecific neighbours within a 10 m radius ($\bar{x} \pm se = 7.9 \pm 0.6$ colonies) in April 1992, and moved them > 75 m from the focal nest.

I excavated the 32 colonies in July of 1993, before the first mating flight of the year, counted all sexual offspring in each colony and determined reproductive output (in grams) by the equation:

$$(\text{Number of males} \times 0.0182) + (\text{Number of females} \times 0.0314) \qquad (1)$$

and investment ratio, R, by the equation:

$$(\text{Number of males} \times 0.0182) / \text{equation (1)}, \qquad (2)$$

where the values 0.0182 and 0.0314 are the mean fresh masses in grams of males and females, respectively (Chapter 2). An R of 0.50 indicates equal investment in each sex, and an $R < 0.50$ indicates female bias.

I estimated the natural supply of invertebrates near control and neighbour-removed colonies in early July 1993. I set in the ground a circular pitfall trap (diameter = 11 cm) containing water and dish soap 2 m from each control or neighbour-removed colony. I collected the traps after 4 d and counted the total number of invertebrates and number of *F. podzolica* and *Myrmica* ants. Ten traps were destroyed by bison.

Data analysis

I report descriptive statistics as means ± one standard error. I used standard inferential statistics to analyze data when variances were homogeneous by the F_{MAX} test (Sokal and Rohlf 1981). Before parametric analyses, I used a log (x) or log (x + 1) transformation of the data. Using ANOVA, I tested the null hypotheses of no difference in foraging distance among species, and no difference in productivity of sexuals and no difference in number of invertebrates between treatments. To locate the significant differences in foraging distance among species, I used Tukey's multiple comparisons test. I used a Kruskal-Wallis test to examine the null hypothesis of no difference among treatments in number of queens under dung. To locate the significant differences in this analysis, I applied a Tukey-type multiple comparison test (Zar 1984). Finally, I did a hierarchical log linear analysis to examine the fate of transplanted colonies.

D. Results

Foraging radius

The maximum foraging radius of workers differed significantly among all species, and on average ranged from 4.69 m for *F. dakotensis* to 16.42 m for *F. subnuda* (Table 4.1).

Foundation experiment

The number of *F. podzolica* queens starting new nests under dung piles differed significantly among treatments. Established colonies of *F. ulkei* and *F. subnuda* prevented foundresses from starting new nests near them, but there was no difference in the number of foundresses under piles of control dung and dung placed around established colonies of *F. podzolica* and *F. dakotensis* (Fig. 4.2). For each treatment, there was no relationship between number of foundresses and distance of dung to established colony (Table 4.2).

Transplant experiment

A model with first and second order effects was adequate to represent the data of the transplant experiment. All first order effects were significant (Survivorship: $G = 93.44$, $df = 1$, $P < 0.000$; Size of transplant: $G = 16.99$, $df = 1$, $P = 0.000$; Treatment [control, conspecific neighbour and heterospecific neighbour]: $G = 44.50$, $df = 2$, $P = 0.000$). Also significant were the survivorship by size of transplant interaction ($G = 19.07$, $df = 1$, $P < 0.000$) and the survivorship by treatment interaction ($G = 29.43$, $df = 2$, $P < 0.000$). Tthe size of transplant by treatment interaction was not significant ($G = 4.06$, $df = 2$, $P = 0.131$). For transplants containing 1 500 workers, survivorship was high in control and *F. podzolica* treatments. However, most colonies were eliminated near established heterospecific colonies. Few transplants containing 50 workers survived across treatments. Survivorship was highest in control colonies, but even so, only 20% survived (Fig. 4.3). There was no difference in survivorship of colonies transplanted either 30 or 150 cm from established colonies, so I pooled these data. Observations revealed that transplants near colonies of *F. dakotensis*, *F. subnuda* and *F. ulkei* were eliminated primarily by their *Formica* neighbours. However, several small, control colonies and small transplants near *F. podzolica* nests were eliminated by *Myrmica* species. One of the small, control transplants to survive was parasitized by a *F. ulkei* queen.

Removal experiment

Total production of alate sexuals did not differ significantly between control and neighbour-removed colonies. In addition, investment ratios were 0.50 and 0.53 for control and neighbour-removed colonies, respectively, indicating colonies invested about equally in each sex. However, sex ratios were male biased (Tables 4.3, 4.4), because males are smaller and weigh less than females (Chapter 2).

The number of invertebrates collected in pitfall traps was not significantly greater in traps near neighbour-removed colonies than those near control colonies. There were fewer *F. podzolica* workers collected in neighbour-removed traps than control traps, but the reverse was the case for *Myrmica* workers (Fig. 4.4).

E. Discussion

In this chapter, I examined three potential ways in which competition affects nest distribution in a guild of formicine ants. I did two experiments using four species to study whether established colonies prevent founding queens of *F. podzolica* from starting new colonies near them, and whether larger colonies eliminate smaller neighbours. In addition, I conducted a removal experiment to test for diffuse competition in *F. podzolica*. Results show that both space preemption of founding queens and interference between established colonies are key mechanisms, the importance of which is contingent upon the neighbouring species. However, I detected no experimental evidence for exploitative competition.

For space preemption to account for observed colony spacing, established colonies must prevent queens from starting colonies near their nests. Workers of many species readily kill or drive away conspecific and heterospecific foundresses upon encounter (Donisthorpe 1927, Pontin 1960, Rockwood 1973, Nickerson et al. 1975, Hölldobler 1981, Nichols and Sites 1991), and because density of foragers tends to be related negatively with distance to the nest, the probability of workers detecting intruders should be greatest near their colony. Hölldobler (1981) demonstrated that success of foundresses of the honey ant *Myrmecocystus mimicus* was indeed related to the distance of established colonies. Queens starting nests within 3 m of established conspecifics were unsuccessful, those starting nests from 3 to 15 m had some success, whereas foundresses initiating nests more than 15 m from established conspecifics were most successful.

In this study, colonizing success of founding queens was dependent on the species of the neighbouring established colony, but was not dependent on distance to the established colony within treatments. Distance to established colony ranged only from 30 to 150 cm (i.e., position of dung piles), though, and this range was well within the area of high foraging activity of each species (Table 4.1). Because workers of *F. ulkei* are very active and aggressive throughout even the warmest days in August, when *F. podzolica* undergo their mating flights (personal observations), they discovered founding queens and prevented them from settling near their nests. Workers of *F. podzolica* are also very active, but are not nearly as aggressive as those of *F. ulkei* (Savolainen and Deslippe unpublished). Although workers of *F. podzolica* readily attack foreign ants placed on their nests, usually they avoid conflict upon encounter while foraging. This behaviour partly explains why queens could start new nests near established conspecific colonies. Because workers of *F. subnuda* are very active and aggressive (personal observations), they, like *F. ulkei*, prevented queens from settling near their nests. However, workers of *F. subnuda* were less successful than those of *F. ulkei* at excluding foundresses, perhaps because their activity in August is strongly diurnal. This activity pattern could allow some foundresses to become established during the afternoon lull, because *F. podzolica* foundresses are extremely active during this period on the day of their mating flights (personal observation). Finally, although workers of *F. dakotensis* are aggressive, they are mostly inactive when temperatures are warm in August (personal observations). As a result, they did not prevent foundresses from establishing new colonies.

Several investigators have studied competition between ant colonies by conducting transplant experiments (Pontin 1969, Bradley 1972, Rosengren 1986, Rosengren et al. 1986), but unlike this study, they did not distinguish between space preemption and interference between mature and immature colonies. In this study, most transplanted colonies were eliminated by species with well developed mass-recruitment systems (i.e., *F. ulkei*, *F. subnuda*, *F. dakotensis* and *Myrmica* spp.). Most surprising, was the elimination of small transplants by *Myrmica* colonies, because myrmicine workers are both smaller compared to those of *F. podzolica*, and subordinate to them at food baits. The myrmicines, however, were as deadly as their formicine counterparts, because they attacked the transplants with armies of nestmates.

Most of the large transplants survived near colonies of *F. podzolica*, perhaps because *F. podzolica* is the one species of those studied that does not have an effective mass-recruitment system. In general, workers forage and return food items to the nest individually. Although there were several instances where I observed a foreign *F. podzolica* worker enter a transplant nest and successfully drag out a worker, workers from large transplants appeared to repel intruders successfully. Because large transplants near *F. podzolica* colonies survived the experimental period, interference between *F. podzolica* colonies is apparently less important than between colonies of *F. podzolica* and other species.

Although space preemption and interference mechanisms account for interspecific patterns of colony spacing, there is no evidence that they account for the uniform dispersion of nests in *F. podzolica.* Consequently, exploitative competition may explain nest spacing in *F. podzolica*, as greater exploitation of limiting resources closer to the colony can produce uniformity through indirect interactions (Johnson et al. 1987). This possibility seemed, *a priori*, particularly likely as patterns in colony abundance, reproductive output and worker headwidths are explained by food supply (Chapters 2, 3). However, the removal experiment failed to support this hypothesis as reproductive output and sex allocation did not differ between control and neighbour-removed colonies. It would be premature to discard the explanation of exploitative competition, though, because (1) extra food made available by removing colonies may have been partly consumed by myrmicines instead of the focal colonies; (2) food may not have been limiting during the experimental period, or (3) it may take several years before effects of removals are detected. In general, exploitative competition has proven difficult to demonstrate experimentally in social insects, but nevertheless, it probably has important effects on both population and community structure in at least some systems (Fellers 1987, Johnson et al. 1987, Hölldobler and Wilson 1990, Savolainen 1991).

F. Summary

1. Although competition is often responsible for patterns of nest spacing in social insects, the way in which competition produces regular spacing is unclear. Potential mechanisms include established colonies (1) killing or repelling founding queens, (2) eliminating neighbouring colonies, (3) killing foragers or inhibiting their foraging activities, and (4) competing exploitatively for a limited resource like food.

2. I conducted field experiments in Elk Island National Park, Alberta, using four species of formicines to test (1) whether established colonies prevent *Formica podzolica* foundresses from starting new colonies near their nests, (2) whether established colonies eliminate small colonies of *F. podzolica* transplanted near their nests, and (3) whether intraspecific, diffuse competition among established colonies of *F. podzolica* affects sexual production and sex allocation.

3. Space preemption of founding queens and interference between established colonies were key mechanisms in all species but *F. podzolica*. The relative importance of these mechanisms was contingent upon the neighbouring species, and understood in terms of species characteristics, particularly activity levels, aggressiveness and development of recruitment systems.

4. Perhaps exploitative competition for food accounts in part for the abundance and distribution of *F. podzolica*. However, a removal experiment failed to produce significant differences in reproductive output and sex allocation between control and neighbour-removed colonies.

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Table 4.1. Mean (± se) maximum foraging radius of *Formica* workers. N is the number of colonies. Foraging radius differed significantly among species ($F_{3,41} = 24.24$, $P < 0.0001$). Different letters designate means that differed at $P = 0.05$. Data were log transformed prior to analysis.

Species	N	Foraging radius (m)	SE
F. podzolica	20	10.18^{a}	0.69
F. dakotensis	10	4.69^{b}	0.58
F. subnuda	5	16.42^{c}	1.59
F. ulkei	10	7.26^{d}	0.55

Table 4.2. Mean (± se) number of *F. podzolica* foundresses under bison dung placed 30 to 150 cm from established colonies. N is the number of replications. Because controls were isolated from established colonies, they were not included in this table.

			Distance to established colony (cm)				
Treatment	N	Total N dung	30	60	90	120	150
F. podzolica	5	100	1.00 ± 0.45	0.40 ± 0.24	1.00 ± 0.63	1.80 ± 1.56	0.80 ± 0.37
F. dakotensis	5	100	1.60 ± 0.81	0.60 ± 0.24	0.80 ± 0.37	1.00 ± 0.32	3.20 ± 1.46
F. subnuda	6	120	0.33 ± 0.21	0.33 ± 0.21	0.00 ± 0.00	0.50 ± 0.22	0.83 ± 0.48
F. ulkei	7	140	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.14	0.00 ± 0.00	0.00 ± 0.00

Table 4.3. Production of sexuals by control and neighbour-removed colonies of *F. podzolica.* R is the investment ratio (mass of males divided by the total mass of sexuals).

	Treatment	
Variable	Control	Neighbours removed
N colonies	16	16
N males	7320	7481
N females	4228	3900
Mass males (g)	133.2	136.2
Mass females (g)	132.8	122.5
Sex ratio (M/F)	1.73	1.92
R	0.50	0.53

Table 4.4. Mean (± se) mass of sexuals produced by control and neighbour-removed colonies of *F. podzolica*. Prior to ANOVA, I used a log (x+1) transformation. Control and treatment means did not differ significantly.

	Treatment			
Variable	Control	Neighbour removed	$F_{1,30}$	P
N colonies	16	16		
Mass males (g)	8.33 ± 1.77	8.51 ± 2.57	0.571	0.46
Mass females (g)	8.30 ± 2.99	7.65 ± 3.27	0.087	0.77
Total mass (g)	16.62 ± 2.34	16.16 ± 2.91	0.002	0.96

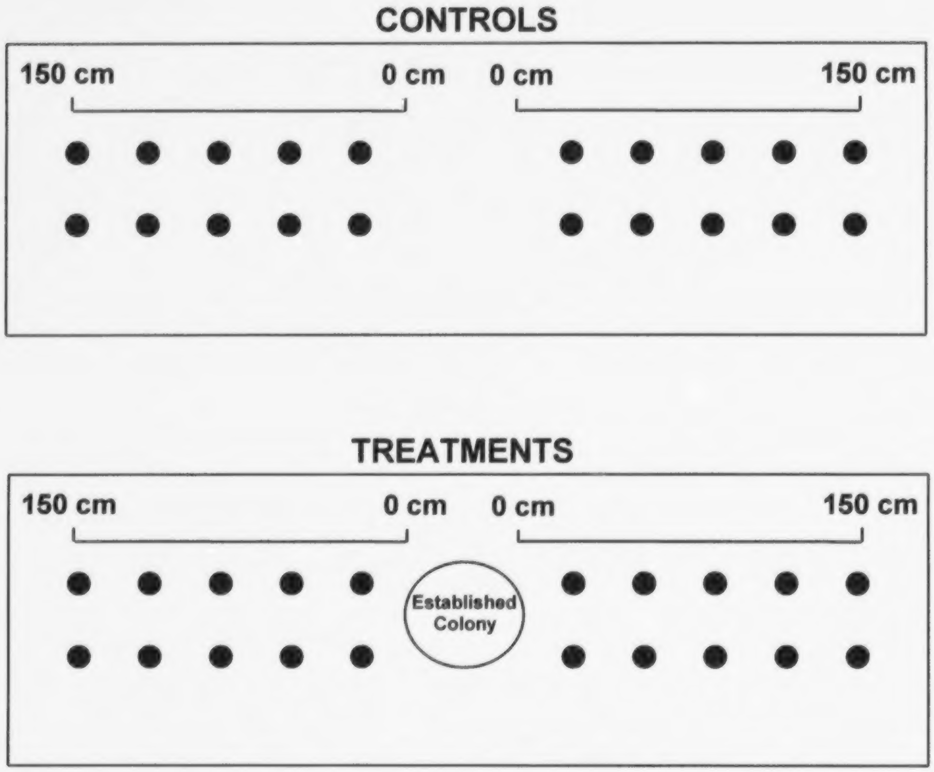
CONTROLS
150 cm
0 cm
0 cm
150 cm
TREATMENTS
150 cm
0 cm
0 cm
150 cm
Established Colony

Fig. 4.1. Diagram of setup of colony foundation experiment. Four rows of five bison dung were placed 0 to 150 cm from established colonies of *F. podzolica*, *F. dakotensis*, *F. subnuda* and *F. ulkei*. Controls were isolated from established colonies.

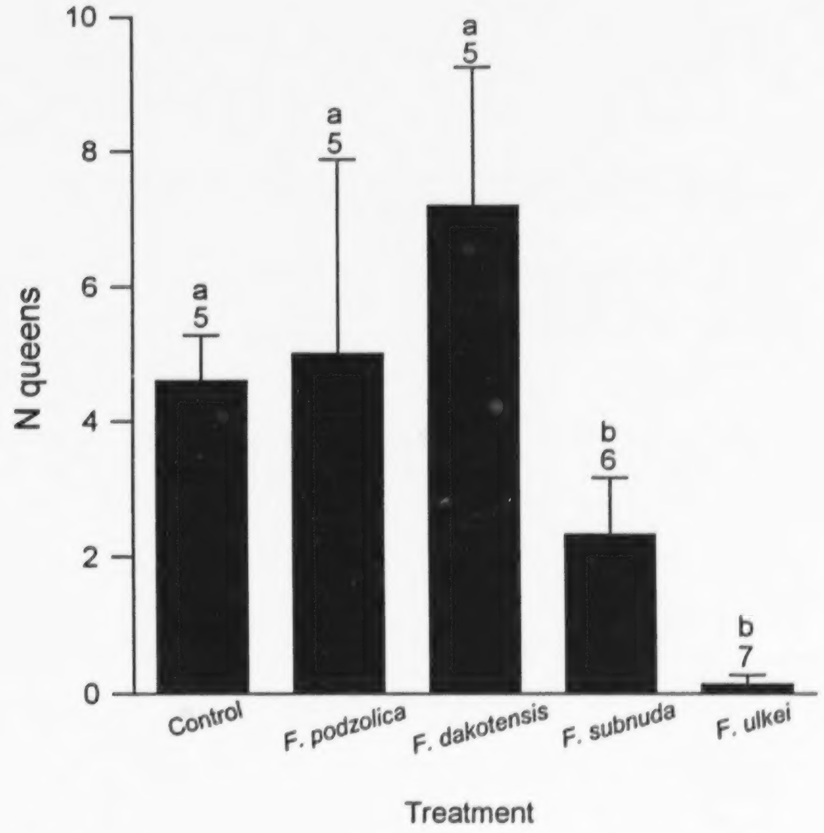

Fig. 4.2. Number of *F. podzolica* queens per 20 piles of bison dung placed around established colonies of *F. podzolica*, *F. dakotensis*, *F. subnuda* and *F. ulkei*. Controls were isolated from established colonies. Mean number of queens differed significantly among treatments (H = 15.69, P = 0.0035). Error bars show one standard error above the mean. Sample sizes are indicated by numbers above error bars. Shared letters designate means that did not differ significantly (Tukey P > 0.05).

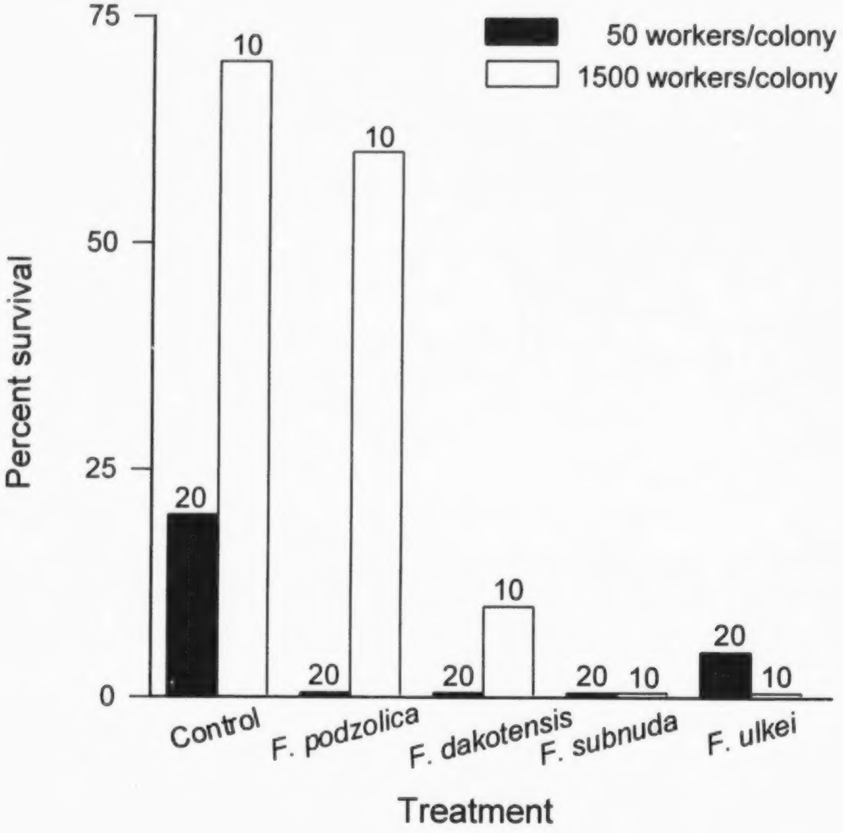

Fig. 4.3. Percent survival of transplanted colonies. Treatments were established colonies of different *Formica* species and size of transplanted colonies. Control colonies were isolated from established colonies. Sample sizes are indicated by number above bars. I present a three-way contingency table analysis of the results in Table 4.3.

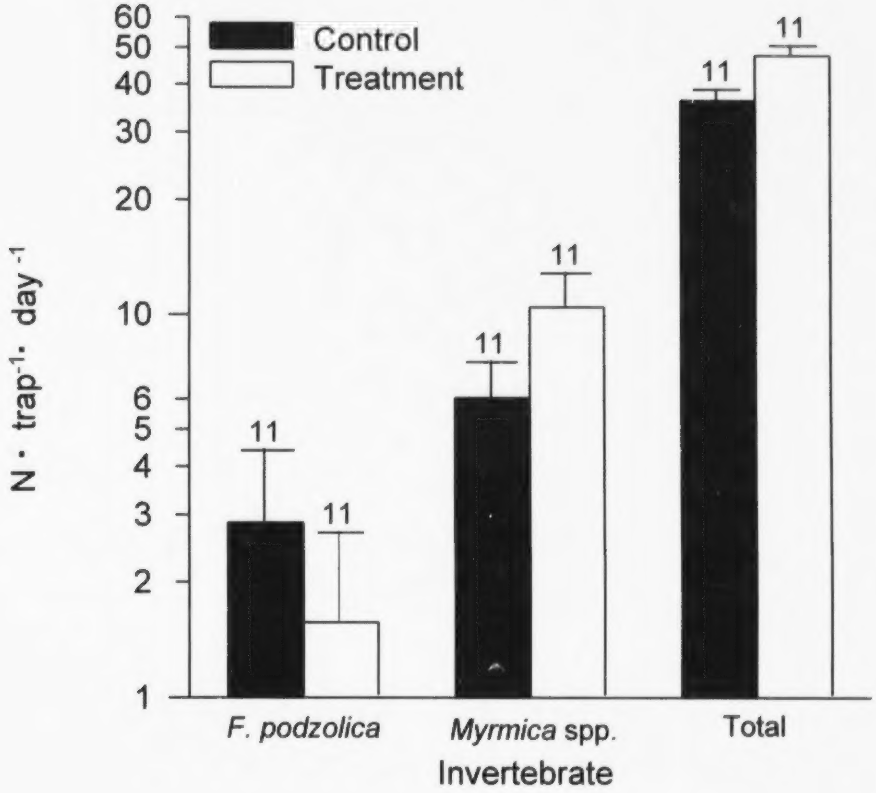

Fig. 4.4. Log number of invertebrates per pitfall trap per day in pitfall traps located 2 m from control and neighbour-removed colonies of *F. podzolica*. Error bars show one standard error above the mean. In ANOVA, $F_{F.\ podzolica} = 2.45$, $P = 0.13$, $F_{Myrmica\ spp.} = 1.60$, $P = 0.22$, $F_{Total} = 1.99$, $P = 0.17$. Sample sizes are indicated by numbers above error bars.

CHAPTER 5

COLONY FOUNDATION AND FACULTATIVE POLYGYNY IN THE ANT, *Formica podzolica*

A. Introduction

Social insects have three distinct parts to their colony life cycles (Oster and Wilson 1978). In the founding stage, mated queens establish new colonies either with or without workers (i.e., by swarming or independent foundation). Establishment by swarming is common in polygynous ants (Keller 1991) and polybiine wasps (Hölldobler and Wilson 1977), and is the sole mode in army ants (Schneirla 1971) and honeybees (Michener 1974). Otherwise, independent foundation predominates in social insects (Wilson 1971). Following the founding stage is the ergonomic phase, in which the colony allocates most of its energy to producing new workers. This phase is characterized by exponential growth persisting for a few months to many years depending on the species (Hölldobler and Wilson 1990). In the last part of its cycle, the reproductive stage, the colony produces alate sexuals that eventually leave the nest to disperse and mate.

Queens are most susceptible to starvation, predation and the vagaries of weather during the founding stage (Whitcomb et al. 1973, Hölldobler and Wilson 1990, Nichols and Sites 1991). Swarming largely eliminates these risks, because queens remain in the presence of worker nestmates that provide them with food, defense against predators and thermal insulation. Although queens colonizing independently remain more exposed than those colonizing dependently, they have evolved other successful strategies to reduce risk of mortality. In ants, for example, queens of several species of ponerines, attines and myrmicines forage for food outside the nest chamber while rearing their first brood (Haskins 1970, Weber 1972, Dejean 1987). Feeding prevents starvation and allows production of a larger initial brood, but it also exposes queens to additional predators. In contrast, queens may be claustral, meaning they do not leave the nest, and rear the first brood in isolation completely on the metabolic breakdown of body tissue. This behaviour reduces the risk of predation, but it also increases the chance of starvation before the first workers emerge. To remain claustral and prevent starvation, founding queens store a higher relative fat content compared to species using either non-claustral or dependent colony foundation (Keller and Passera 1989), they may cooperate with other queens (Rissing and Pollock 1988), or they may parasitize an established nest and be served by the host workers (Buschinger 1986).

Considerable variation both within and among colony stages occurs in the number of mated queens in a nest, and in the way the variation is produced (Hölldobler and Wilson 1977, 1990). One to several queens may be present in the founding stage, depending on whether colonies are established by one (i.e., haplometrosis) or more than one queen (i.e., pleometrosis). Similarly, a mature nest may contain a single queen or a few to many queens, termed monogyny, oligogyny or polygyny, respectively. Multiple queens in mature nests are not necessarily original foundresses, because colonies may fuse or queens may be adopted into nests (i.e., secondary pleometrosis). Either only one queen is a functional egg-layer (i.e., functional monogyny), or multiple queens are egg-layers (i.e., functional polygyny).

To gain insight into cooperative behaviour, several investigators have compared the development of colonies or behaviours of queens in colonies founded by pleometrosis and haplometrosis (Waloff 1957, Bartz and Hölldobler 1982, Tschinkel and Howard 1983, Hölldobler and Carlin 1985, Packer 1986, Rissing and Pollock 1986, 1987, Mintzer 1987). In species studied to date, pleometrosis is usually common, and mature nests are either monogynous or oligogynous. Little is known of the comparative population structure in ants with alternate ways of founding nests (Rissing and Pollock 1988). In addition, there has not been a detailed study comparing colonies founded by pleometrosis and haplometrosis when there is large variation in queen number in all stages of colony development. I help to fill these gaps in this study. My objectives were to document the variation in number of queens occurring naturally in founding, immature and mature nests of the ant *Formica podzolica,* and to compare experimentally development of colonies and survivorship of queens in colonies of *F. podzolica* founded with 1 to 16 queens.

B. Materials and methods

Formica podzolica ranges widely in North America (Francoeur 1973), and is the numerically dominant *Formica* ant in central Alberta. It is a medium-sized, black ant that serves as host to several parasitic ants. Colonies nest primarily in soil along forest edges and in meadows, and they form conspicuous mounds, the largest of which exceed 2 m in diameter (Chapter 2). I estimate that colonies producing alate sexuals typically contain between 5 000 and 40 000 workers, and the largest ones exceed 100 000 workers. Workers tend homopterans for honeydew, and they scavenge and prey on various invertebrates from March to October. Several nuptial flights occur per year, beginning in late July and ending in early September before the onset of winter.

To determine the number of queens occurring naturally in nests at each stage of colony development, I excavated founding, immature and mature colonies of *F. podzolica*. Only nests with at least one queen were included in the data set. I classified colonies as founding if only queens were present, immature if there were workers, but no production of sexuals, and mature if colonies were producing sexuals. In addition, I classified a colony as monogynous, oligogynous, polygynous or strongly polygynous if it contained 1, 2-5, 5-10 or >10 queen(s), respectively. I conducted the excavations from 1990 to 1993 in Edmonton and Elk Island National Park, Alberta, Canada.

To compare development of colonies and survivorship of queens in nests founded by haplometrosis and pleometrosis, I established nests of *F. podzolica* initially containing 1, 2, 3, 4, 8 or 16 queens in the lab. I collected foundresses in Edmonton, Alberta, on August 7 and 8, 1991, as they were searching for a nesting site following a mating flight. I weighed the queens on a Mettler P162™ balance, and placed them in 1 of 216 artificial nests. The nests were made by joining the lips of two bottom petri plates (9.0 cm by 1.8 cm) and sealing them with masking tape. Glued in the bottom center of each nest was the bottom of a smaller petri plate (5.5 cm by 1.4 cm) containing a moistened ball of cotton.

I placed the nests in an incubator at the University of Alberta set at 30°C, except for 105 days in the middle of the study period when I kept the incubator at

5°C. The study was initiated on August 8, 1991, and ended February 24, 1992, after the first week in which some nests produced workers. During the study, I regularly monitored acts of cooperation and hostility, mortality of queens, distribution of eggs, and production of eggs, larvae, pupae and workers. I removed dead queens from the nest, and weighed the surviving ones at the end of the experiment. To mimic the natural condition, no food was provided to the foundresses, so the first brood was reared entirely on body reserves.

I report descriptive statistics as means ± one standard error, and used standard inferential statistics to analyze data when variances were homogeneous by the F_{MAX} test. Using log-likelihood tests, I tested the null hypotheses of no association between gyny of nests and stage of colony development, and between number of eggs and number of egg clumps per nest. With ANOVA and Tukey's multiple comparison tests, I tested the null hypotheses of no difference in weight loss and no difference in number of pupae among treatments differing in initial number of foundresses. Finally, I used Kruskal-Wallis tests to examine the null hypotheses of no difference in maximum production of eggs, larvae and pupae among treatments. To locate the significant differences in the Kruskal-Wallis analyses, I applied Tukey-type multiple comparison tests (Zar 1981).

C. Results

The number of *F. podzolica* queens per nest was dependent on stage of colony development (Fig. 5.1). Most colonies were monogynous, but 23.4% of immature and mature nests were oligogynous, polygynous, or strongly polygynous. Occasionally, I found many queens, up to 84 and 140 in an immature and a mature colony, respectively. These colonies were likely functionally polygynous. First, I observed many more worker larvae and cocoons in polygynous than monogynous nests of similar size. Second, queens always proved to be functional egg-layers whenever I kept them in containers separated with workers. Colony establishment was usually by haplometrosis, but pleometrosis occurred in 27.2% of founding nests (Fig. 5.1). However, foundress groups were small ($\bar{x}$ = 1.47 ± 0.04 queens/nest, range = 1 to 8), and therefore, the many queens in some immature and mature colonies did not result from initially large foundress associations.

My lab experiment revealed substantial hostility among foundresses. I regularly observed fighting among them, and mortality of both nests and queens was greater in pleometrotic than haplometrotic nests (Table 5.1). Mortality of nests and queens ranged from 5.9% to 37.5% and 5.9% to 90.4%, respectively, and up to 31.6% of dead queens within a treatment were dismembered (Table 5.1). Queen mortality correlated positively with initial number of foundresses in a nest, and occurred constantly throughout the study except when I maintained temperature at 5°C (Fig. 5.2).

Besides mortality of nests and queens, hostility among foundresses negatively affected body weight. Of queens surviving the experimental period, those from haplometrotic nests maintained significantly more weight than those from pleometrotic nests (Fig. 5.3). Queens founding by themselves lost 8.38 ± 0.60 mg (25.26% of initial weight, n = 16), whereas those founding with others lost from 10.52 ± 0.61 to 13.36 ± 0.84 mg (31.92%, n = 10 and 40.30%, n = 13 of initial weight) depending on the treatment (Fig. 5.3).

Despite the observed hostility among foundresses, queens also cooperated and cohabited peacefully. Pleometrotic queens were usually aggregated, and they seemed to contribute about equally to egg laying, brood care and social grooming. In addition, foundresses did not keep separate egg masses. Although the proportion of nests with two or more clumps was greater when the maximum number of eggs in a nest was more than 30, queens usually kept eggs in a single clump when the maximum number was 30 or less (Table 5.2).

Cooperation among foundresses sometimes overcame the negative effects of their hostility, and small foundress associations showed the greatest benefits. The maximum numbers of eggs, larvae and pupae were significantly different among treatments, and were greater in multiple foundress associations (Fig. 5.4). However, oophagy and cannibalism of larvae were high in treatments of 8 and 16 queens per nest. Therefore, groups of 2 to 4 queens produced more pupae than other treatments (Fig. 5.4.) Of nests that produced pupae, though, production did not differ significantly among treatment groups (Fig. 5.5).

D. Discussion

In this chapter, I compared the number of queens occurring naturally in founding, immature and mature colonies of *F. podzolica*, and conducted a lab experiment to study colony foundation. My results show that pleometrosis is common. However, foundress groups are small, and large artificial groups experience high mortality in laboratory nests. Consequently, strongly polygynous colonies are probably secondarily pleometrotic. Perhaps colonies adopt foundresses after mating flights as in *Formica ulkei* (Scherba 1958) and *Iridomyrmex purpureus* (Hölldobler and Carlin 1985). If so, they may be adopting foreign queens in *F. podzolica*, because Bennett (1986) showed that relatedness among nestmates is low and genetic variation within mature, polygynous colonies is greater in this species than in a related, monogynous species, *F. argentea*. Another possibility is that nests join as occurs sometimes in polygynous acacia ants (Janzen 1973). I often have observed several groups of *F. podzolica* queens starting nests under the same clump of turf or pile of bison dung, and found incipient nests concentrated locally. As a result, conditions exist in the field to facilitate fusion of nests.

On a further speculative note, the supernumerary queens in immature and mature nests may behave as conspecific parasites. In Elk Island National Park alone, *F. podzolica* is host to two temporary social parasites (*F. dakotensis* and *F. ulkei*), a facultative slave-maker (*F. subnuda*) and two obligate slave-makers (*F. subintegra* and *Polyergus breviceps*) (Savolainen and Deslippe unpublished). Because *F. podzolica* is readily parasitized by other species, and nestmate recognition is primarily learned rather than assessed based on genotypically correlated labels (Bennett 1989a,b), it may likewise be susceptible to parasitism by conspecific queens. Based on the absolute number of queens and the queen to worker ratio in polygynous colonies, Elmes (1973) has similarly suggested that supernumerary queens of *Myrmica rubra* exist as parasites on colonies that accept them.

I found greater production of eggs, larvae and pupae in pleometrotic than haplometrotic nests, a result consistent with previous studies (reviewed in Rissing and Pollock 1988). However, fighting among *F. podzolica* queens was common and often led to death, particularly in large foundress associations. Rates of fighting and mortality were intermediate to those documented in haplometrotic (Hölldobler and Carlin 1989) and other pleometrotic species (Mintzer 1979, Bartz and Hölldobler 1982, Rissing and Pollock 1986, 1987). Furthermore, mortality was constant throughout the founding stage in pleometrotic groups, whereas in other pleometrotic species, it is almost absent except when queens first join a group, and once they produce workers (Bartz and Hölldobler 1982, Rissing and Pollock 1987). I ended my study before most nests produced workers, so I do not have data on rate of queen mortality as colonies moved into the ergonomic stage. However, other investigators have studied this period more carefully in *Messor pergandei* (Rissing and Pollock 1987, 1991), *Myrmecocyctus mimicus* (Bartz and Hölldobler 1982) and *Solenopsis invicta* (Tschinkel and Howard 1983, Tschinkel 1992a,b, in press). Only a single foundress of the original group usually survives, because either queens fight to the death, or workers kill all but one foundress and pilfer the brood.

It has become apparent that there are two important differences between pleometrosis in wasps and ants (Rissing and Pollock 1988, Strassmann 1989). Unlike ants, wasp queens in groups tend to be related and they establish dominance hierarchies (Packer 1986, Pratte 1990). My findings concur with those of previous studies of ants that show kin selection is unlikely (Hagen et al. 1988, Rissing and Pollock 1988), and hierarchies, if present, are subtle (Mintzer 1979, Rissing and Pollock 1986). As a pilot study in 1990, I mixed foundresses collected over 40 km apart, and results on survivorship and antagonistic behaviour of pleometrotic queens were consistent with the ones I report in this paper. In addition, queens did not form obvious hierarchies.

The number of queens in ant colonies varies considerably among colony stages, and within and among species. When queens are unrelated, polygyny presents an evolutionary paradox, because genetic relatedness among colony members and personal reproduction is lowered. To address this paradox, several hypotheses and more formal cost-benefit models have been developed (Janzen 1973, Hölldobler and Wilson 1977, Bartz and Hölldobler 1982, Nonacs 1989). However, although our understanding of polygyny has been advanced substantially in the past decade (Hölldobler and Wilson 1990), it remains inadequate. Additional research on reproductive structure and dynamics of queen numbers over the course of colony development should produce further advances.

E. Summary

1. To gain insight into cooperative behaviour, I documented the variation in number of queens occurring naturally in founding, immature and mature nests of the ant *Formica podzolica*, and compared development of colonies and survivorship of queens in experimental nests started with 1 to 16 foundresses.

2. Number of queens per nest was associated with stage of colony development. Most nests were monogynous, but 23.4% of immature and mature nests (n=158) were oligogynous or polygynous. Colonies were usually establishment by single queens (i.e., haplometrosis), but establishment by multiple queens (i.e., pleometrosis) was also common, occurring in 27.2% of founding nests (n=492).

3. Foundress groups in the field were small ($\bar{x} = 1.47 \pm 0.04$ queens/nest), and large groups experienced high mortality and low productivity in artificial nests. As a result, the many queens (up to 140) in some immature and mature colonies were secondarily pleometrotic. I argued that these supernumerary queens may be conspecific parasites.

4. My experiment on colony foundation revealed both costs and benefits to pleometrotic associations, and that small groups (2 to 4 queens) produced more pupae than larger groups (8 or 16 queens) or single foundresses.

5. Although foundresses cooperated and cohabited peacefully, they were often hostile in large groups. Queens in pleometrotic associations lost more weight and suffered greater mortality compared to single foundresses due to antagonistic behaviour. Rate of queen mortality correlated positively with initial number of queens in a nest, and was constant throughout the study, except when I maintained temperature at 5°C. Compared to previous studies on colony establishment in ants, rate of mortality was intermediate between haplometrotic and other pleometrotic species.

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Table 5.1. Mortality of nests and queens and percent of dead queens dismembered in nests started with 1 to 16 queens of *F. podzolica*.

	N queens per nest					
	1	2	3	4	8	16
Initial N nests	17	16	17	16	16	15
Final N nests	16	15	14	10	12	13
% nest mortality	5.9	6.3	17.7	37.5	25.0	13.3
Initial N queens	17	32	51	64	128	240
Final N queens	16	24	32	22	32	23
% queen mortality	5.9	25.0	37.3	65.6	75.0	90.4
% dismembered	0.0	37.5	31.6	23.8	18.8	19.4

Table 5.2. Log-likelihood test of number of egg clumps per nest and maximum number of eggs observed in nests started with 1 to 16 *F. podzolica* queens.

		N egg clumps/nest	
		1	> 1
N eggs/nest	≤ 30	41	15
	> 30	8	15

$G_{adj} = 10.10$, df = 1, $P < 0.002$

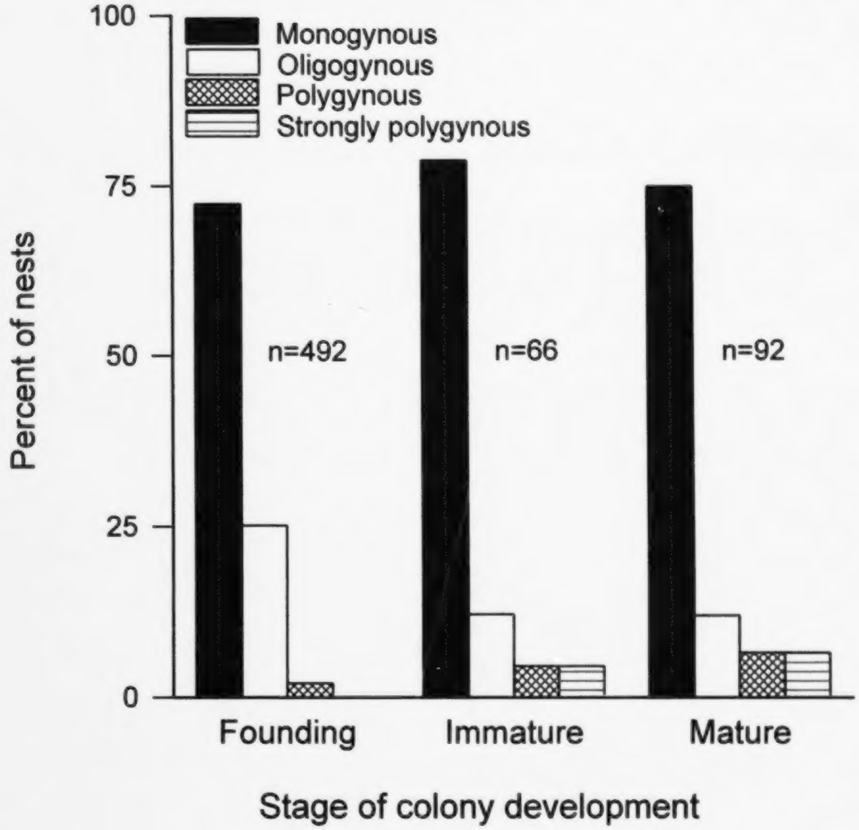

Fig. 5.1. Percent of nests of *F. podzolica* that were monogynous, oligogynous, polygynous and strongly polygynous at the founding, immature and mature stages of colony development. Gyny of nests was associated with stage of colony development ($G_{adj} = 41.86$, df = 6, $P < 0.001$).

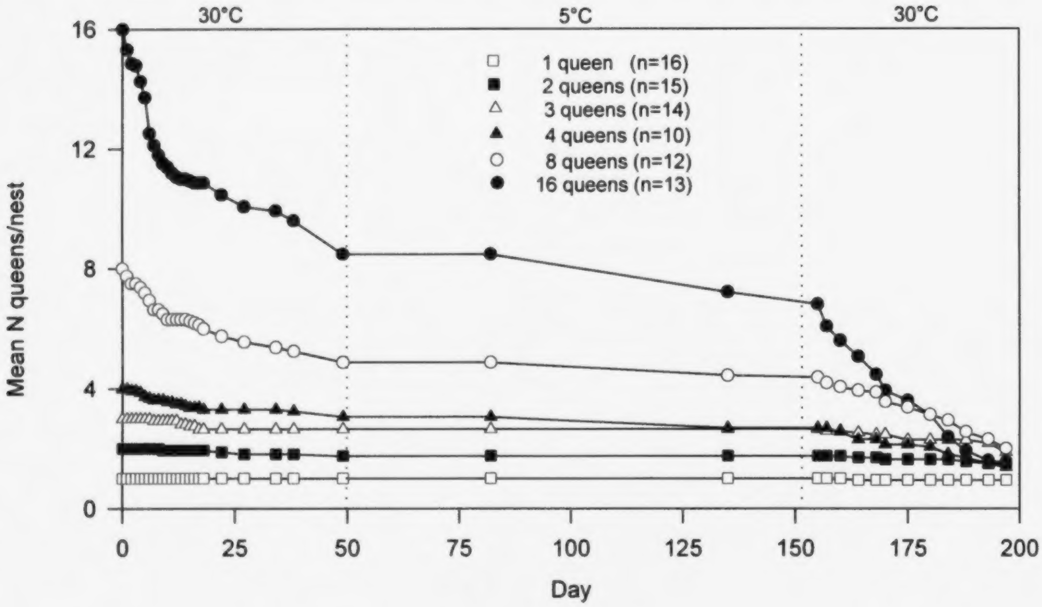

Fig. 5.2. Mean number of *F. podzolica* queens per nest from colony foundation until first nests produced workers in nests started with 1 to 16 queens. There was little to no mortality when temperature was 5°C, but in nests initially containing 8 and 16 queens, mortality was high and rate was constant when temperature was 30°C.

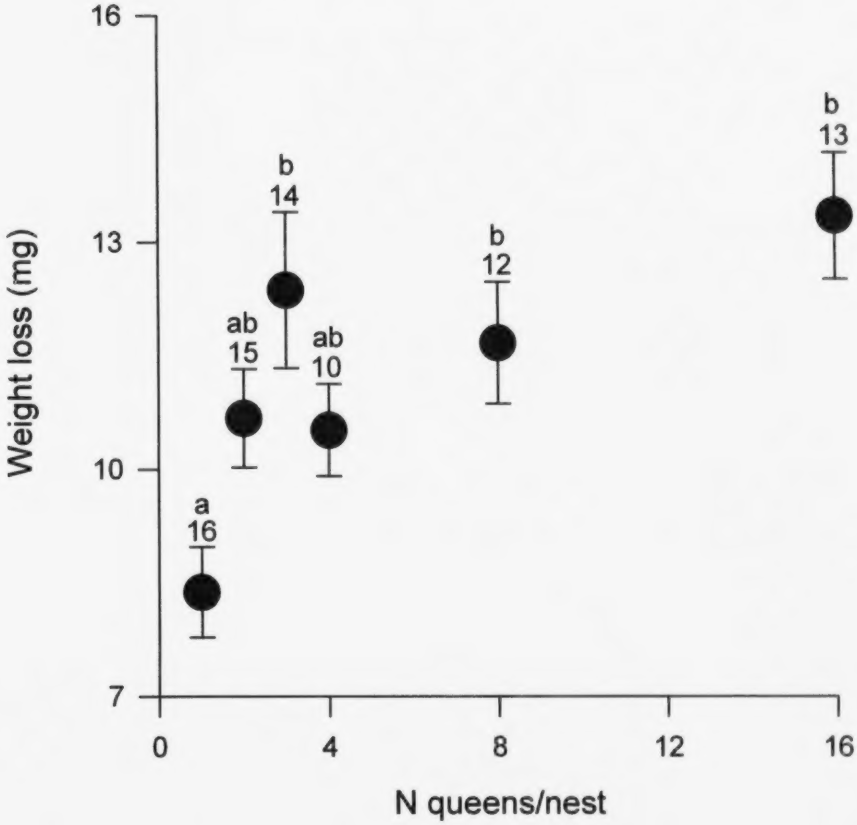

Fig. 5.3. Weight loss of *F. podzolica* queens from colony foundation until first nests produced workers in nests started with 1 to 16 queens. Error bars show one standard error above the mean. Weight loss differed significantly among treatments ($F_{5, 79} = 5.06$, $P < 0.001$). Sample sizes are indicated by numbers above error bars. Shared letters designate means that did not differ significantly (Tukey $P > 0.05$).

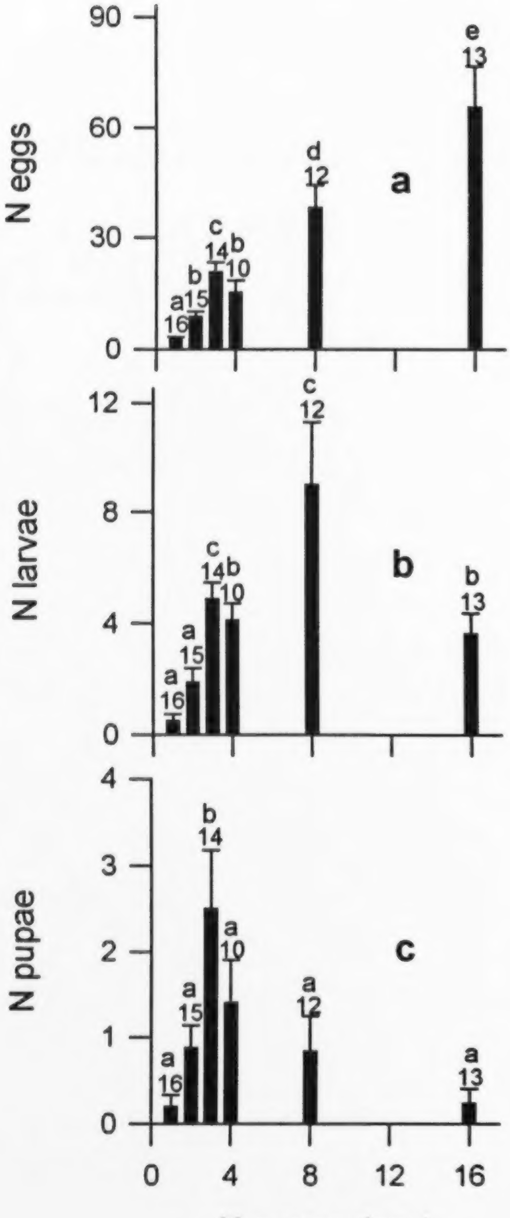

Fig. 5.4. Maximum number of (a) eggs, (b) larvae and (c) pupae observed until first nests produced workers in nests started with 1 to 16 *F. podzolica* queens. Production differed significantly among treatment groups (eggs: H = 56.22, $P < 0.001$; larvae: H = 34.65, $P < 0.001$; pupae: H = 17.85, P = 0.003, all df = 5). Sample sizes are indicated by numbers above error bars. Shared letters designate means that did not differ significantly (Tukey $P > 0.05$).

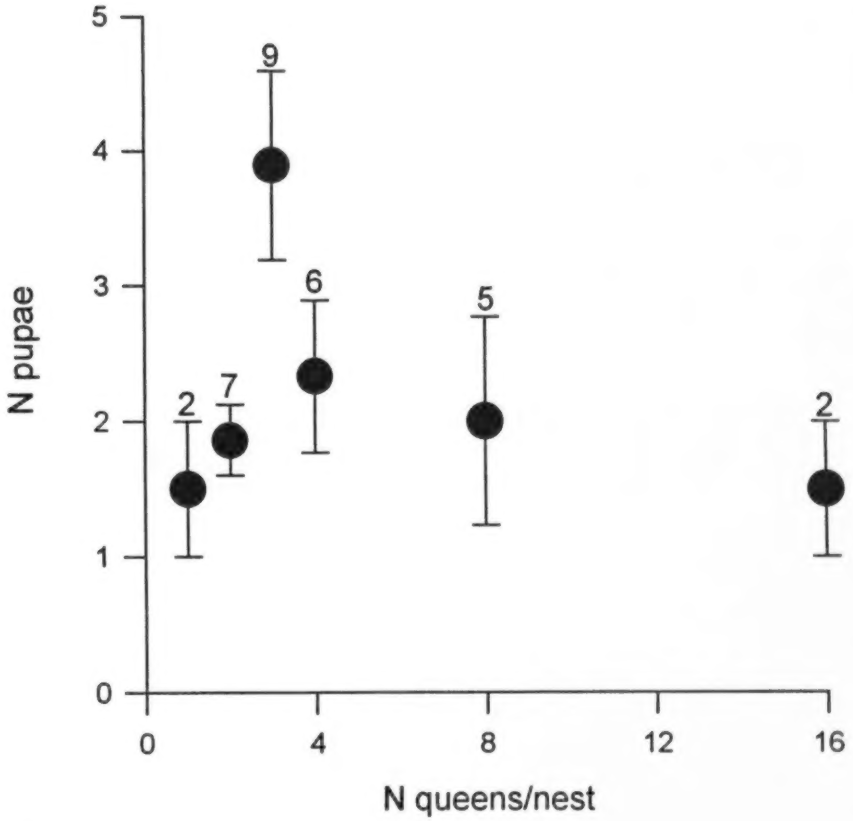

Fig. 5.5. Mean number of pupae across treatments in nests of *F. podzolica* with at least one pupa before the first nests produced workers. Production did not differ significantly among treatment groups ($F_{5, 30}$ = 2.14, P = 0.094). Sample sizes are indicated by numbers above error bars.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSION

A. General framework

In theory, the importance of both intra- and interspecific competition should depend on the trophic position of the species. Hairston et al. (1960) argued that it should be greater in autotrophs, decomposers and carnivores, compared to herbivores. This conclusion follows from the premise that autotrophs, decomposers and carnivores are limited by the amount of solar energy, the quantity of dead tissue, and the supply of herbivores, respectively, whereas herbivores, occupying an intermediate position in the food web, are more likely to be regulated by predators. This association between competition and position in the food web has been reasonably well supported by many empirical studies (Connell 1983, Schoener 1983, Fowler 1986, Keddy 1989, Goldberg and Barton 1992, Gurevitch et al. 1992).

Besides trophic position, the importance of competition should depend on characteristics of particular species within each trophic level (Schoener 1983, 1986). Long life and large body size are two of the key traits promoting intense competition, since large and long-lived species typically resist predation. Such species should saturate suitable habitats until some resource like food or nest sites become limiting and competition becomes a major density-dependent factor. Because social insects are secondary consumers and have large, long-lived colonies that resist predation, their populations and communities should be organized in large part by competition. In reality, the process is a major force in this group and cannot be dismissed as a fad or an artifact of procedures (Hölldobler and Wilson 1990).

Body size (colony size in social insects) and associated measures like stage of the life cycle are also important to consider within a species, because size discrepancies among individuals affect the nature and outcome of interactions (Wootton 1993). For example, one might expect competition between two equally matched opponents to be a long and drawn out affair with both parties suffering substantial losses in fitness. Conversely, one expects competition to be asymmetrical between large and small individuals, with larger ones having the upper hand. When size discrepancies are very large, as often occurs in size-structured populations, survivorship bottlenecks are common due both to competition and intraguild predation (Polis et al. 1989). These bottlenecks can exert great selective pressure on individuals to develop through them as rapidly as possible.

B. Summary of findings and significance

In this dissertation, I investigated the nature of resource limitation and competition in a population of the ant *Formica podzolica* to understand more clearly patterns of distribution and abundance. I used a combination of descriptive, comparative and experimental studies, and in most comparisons, controlled for either colony size or stage of the life cycle. First, I examined associations between habitats that differed in natural food supply and colony abundance, distribution, productivity, sex investment and size of colony members. In addition, I compared productivity and sex investment of colonies supplemented and not supplemented with food (Chapters 2, 3). While collecting information on the relationship between food supply and sexual production (Chapter 2), I had to collect data on production of both males and females. It was a simple matter, therefore, to consider these individual components and study the relationship between food supply and sex allocation. I treated this matter in a separate chapter as it was of special theoretical interest (Chapter 3).

I began with a consideration of food resources, because any study of a population or community should consider resources (Price 1984), and resource limitation should be shown before attributing results to competition (Keddy 1989). All measured variables (except size of sexuals) differed significantly across habitats, and they were positively associated with food levels across habitats (Chapters 2, 3). These results suggest that food supply has a major role in structuring this population, and that colonies respond to food addition even within one reproductive cycle.

Second, I conducted three field experiments to test for competition, and to decipher mechanisms of competition (Chapter 4). In this study, I expanded the scope to include both intraspecific and interspecific interactions, because I wanted a more thorough picture of the forces acting on the population of *F. podzolica*. Specifically, I tested whether established colonies prevent foundresses from starting new colonies near their nests, whether they eliminate small colonies transplanted near their nests, and whether they compete exploitatively for food. A removal experiment failed to produce significant differences in reproductive output and sex allocation between control and neighbour-removed colonies (Chapter 4). However, survivorship was significantly affected by interference competition between colonies of *F. podzolica* and three other *Formica* species. Space preemption of founding queens and/or interference between established colonies were key mechanisms in all species but *F. podzolica*. The relative importance of these mechanisms was contingent upon the neighbouring species, and understood in terms of species characteristics, particularly activity levels, aggressiveness and development of recruitment systems (Chapter 4).

From this work and the results of other projects (Savolainen and Deslippe unpublished), it was apparent that the founding and early ergonomic stages represent survivorship bottlenecks due largely to both competition and social parasitism. Because these stages are so critical to a colony, I wanted to uncover strategies *F. podzolica* may employ to develop through them more rapidly. One strategy involves cooperation of queens during colony foundation. In the final project, I compared development of colonies and survivorship of queens in experimental nests started with 1 to 16 foundresses (Chapter 5). Small groups (2 to 4 queens) had less mortality than larger groups (8 or 16 queens), and produced more pupae than larger groups or single queens before the first nests produced workers. Compared to previous studies on colony establishment in ants, rate of mortality was intermediate between haplometrotic and other pleometrotic species.

The research reported in this dissertation contributes to an understanding of the organization of an ant population. As such, it permits direct comparisons of similarities and differences among populations, an endeavor that leads to a greater understanding of ecological and evolutionary processes. In addition, it is one of the more thorough ecological investigations of *Formica* ants. Such studies are rare because these ants typically form large, populous colonies, and their study is labour intensive. In contrast, except for pest species like fire ants (*Solenopsis* spp.) (Lofgren and Vander Meer 1986), most species well examined both within and across colonies and populations have small colonies like *Leptothorax* spp. and *Myrmica* spp. (Elmes 1987a,b, Alloway et al. 1982, Elmes and Wardlaw 1982, Herbers 1983, Herbers 1990). More specifically, the research reported in this dissertation provides the first study to distinguish experimentally between space preemption and interference competition, and is the first to demonstrate experimentally that food has a key proximate role in determining sex investment in field populations. It also adds new insight on the dynamics of cooperation and conflict among queens during colony foundation.

C. Speculations on system dynamics

During this research, I developed the distinct impression that the concept of succession goes a long way towards explaining the dynamics of the formicine host-parasite system in Elk Island National Park. Although some evidence is lacking and much of it is circumstantial, in this section I piece together the tidbits of information to produce a picture of the system dynamics. I begin with a brief overview of succession, then apply the concept to the study system.

Succession describes changes in a community following either disturbance or the colonization of newly exposed substrate. Pioneering species adapted to the disturbed habitat are successively replaced by others until the community reaches a final stable association, the climax. Early stages tend to be dominated by poor competitors with short life cycles that can establish quickly. In contrast, climax species tend to be superior competitors that grow more slowly and express their dominance only after others have developed and reproduced. The processes that govern succession are facilitation, inhibition and tolerance (Connell and Slatyer 1977). The terms refer to the effect of one established species on the probability of colonization of a second, potential invader.

Formica podzolica has characteristics typical of pioneering species. Colonies are poor competitors compared to the other formicines in the system (Chapter 4), and they participate in several mating flights per year. They produce many sexual offspring (Chapter 2, 3) that disperse widely, and this combination rapidly leads to colonization of new substrate. Cooperation among founding queens and perhaps nest fusion accelerates colony development (Chapter 5), and these strategies lead to the quick saturation of a habitat. Furthermore, *F. podzolica* is a habitat generalist, occurring commonly in forests, along forest edges, in meadows and in bogs (Chapter

2). Because later successional species have narrower habitat niches (i.e., largely restricted to forests, forest edges and lake margins), at the very least, colonies of *F. podzolica* find refuge in meadows and continue to produce sexual offspring ready to colonize any new substrate created by disturbance.

Formica podzolica is a necessary precursor of the later successional formicines, or in the terms of Connell and Slatyer (1977), it facilitates their establishment. This facilitation occurs because each of the later successional formicines is parasitic on *F. podzolica* at the colony founding stage. Namely, the temporary social parasites, *F. ulkei* and *F. dakotensis*, the facultative slave-maker, *F. subnuda*, and the obligate slave-makers, *F. subintegra* and *Polyergus breviceps*, each start new nests by penetrating colonies of *F. podzolica* and securing adoption, usually by killing the host queens and assimilating their colony odors.

The nature of parasitic and competitive interactions among colonies is dependent on either host size or size asymmetries. First, only some *F. podzolica* nests are parasitized at the colony founding stage, and only small nests are successfully penetrated (personal observation). Second, competition between large and small colonies is asymmetrical with large ones winning the battles quickly (Chapter 4). Third, although obligate slave-makers may efficiently eliminate large host colonies during slave raids, the more abundant facultative slave-maker, *F. subnuda*, successfully raids only relatively small colonies (Savolainen and Deslippe unpublished manuscript). Finally, large colonies of *F. podzolica* may coexist with the very aggressive parasitic species for many years, because they resist attack of their nests, workers have large foraging ranges and avoid encounters during foraging, and they forage individually and locate food quickly (Chapter 4). Since many colonies of *F. podzolica* become well established in an area before the parasites arrive, the result of size-dependent interactions is a very long transition period from early to late successional stages.

The parasitic species are superior competitors, for they are aggressive, form populous colonies, and have well-developed recruitment systems allowing them to monopolize food sources and attack competitors with organized armies (Chapter 4). They can slowly come to dominate an area, because once colonies become established and mature, they eliminate neighbours and propagate by budding.

Should colonies be unable to eliminate *F. podzolica* neighbours, they will likely outlive them, for their colonies are polygynous and potentially immortal as queens are replaced by their daughters.

The habitat requirements of the temporary social parasites are specialized. For instance, *Formica dakotensis* prefer bogs, and areas overgrown with vegetation, whereas *F. ulkei* prefers forest edges and areas along permanent water bodies (personal observation). In contrast, the slave-makers have more flexible habitat requirements, because their slaves expand both their feeding and habitat niches (Savolainen and Deslippe unpublished manuscript). Indeed, the nests and niches of the obligate slave-makers are nearly identical to those of *F. podzolica,* for their slaves are nearly exclusively responsible for nest maintenance and all foraging except that associated with slave raids (Savolainen and Deslippe unpublished manuscript).

D. Prescriptions

Several additional studies on this formicine system would make good follow-up projects to the research reported in this dissertation. I conclude with a brief discussion of two of the more interesting possibilities. One involves a novel test of a sex allocation hypothesis, and the other involves mechanisms of host-parasite interactions.

Sex investment in a facultative slave-maker

As I explained in Chapter 3, population sex investment of social hymenopterans should approach a 3:1 female-biased ratio under worker control due to relatedness asymmetries among colony members. However, worker control is unlikely in slave-making ants when slaves raise the brood. When the brood is totally reared by slaves, queens are expected to achieve their preferred 1:1 ratio of sex investment (Trivers and Hare 1976). To date, sex ratios in slave-makers have been examined only in obligate slave-makers (Nonacs 1986, Bourke 1989). A more powerful test would involve comparing sex investment of colonies with and without slaves within the same species. Such a test is possible in facultative slave-makers.

Formica subnuda and its *F. podzolica* slaves are excellent subjects for a test of the genetic relatedness hypothesis, because *F. subnuda* is very common, its colonies are manageable (about 5 000 workers per colony), and I have examined sex investment in *F. podzolica* independent of slavery (Chapter 3). One could begin a study by comparing sex investment in colonies with and without slaves. By excavating colonies and counting colony members, it would be easy to determine relationships among worker number, slave number, queen number and sex investment. One could then study the system experimentally in the lab or the field, for *F. subnuda* readily accepts *F. podzolica* cocoons and permits them to develop. Since *F. subnuda* may consume much of the slave brood (personal observation), and food affects sex investment (Chapter 3), it would be important to distinguish between food levels and the presence of slaves. A good experimental design could have treatments that include fed and unfed colonies with and without slaves.

Mechanisms of host-parasite interactions

Social parasitism is very common in nature, and its study has revealed great diversity and complexity (Buschinger 1986). Many variations on the basic modes of parasitism (i.e., temporary social parasitism, slave-making and inquilism) representing almost every conceivable evolutionary stage have been described (Hölldobler and Wilson 1990). The phylogenetic distribution of the phenomenon is patchy, and as a rule, parasitic species resemble their host species more closely than they do any other. At a more mechanistic level, the parasites exploit the nestmate recognition systems of their hosts using allomones, chemical substances of glandular origin used in communication that elicit behavioural or physiological responses by acting as chemical messages. For example, slave-makers use a special group of alarm allomones during slave raids to panic their target colonies, and queens use cuticular hydrocarbons to deceive and control their hosts. Despite the prevalent use of allomones, however, enormous gaps remain in our knowledge of the way the substances are used and their functions (Hölldobler and Wilson 1990).

Consequently, it would be useful to investigate the nature of chemical interactions between social parasites and hosts, and determine the traits that make some species and colonies more susceptible to social parasitism. Specific questions that could be addressed include: (1) how do queens penetrate host colonies and secure control, and are these mechanisms a function of the mode of social parasitism? (2) what is the nature of alarm allomones used by slave-makers to panic host colonies and secure control? (3) why are slaves of obligate slave-makers much more aggressive than non-slaves of the same species? And (4) what is the relationship between susceptibility to parasitism and the number of host queens per nest? The research would contribute to an understanding of how some signal systems work and how they have evolved.

These questions could be addressed in the same formicine system I researched for this dissertation. To analyse alarm allomones, one could use the established techniques of gas chromatography and mass spectrometry. These allomones are the easiest of all allomones to identify chemically because of their high volatility and low molecular weight. However, many compounds may be involved, and they may act in concert. To determine their functions and thresholds, one would need to develop and conduct several behavioural bioassays in both the lab and field. Finally, to examine the relationship between susceptibility to parasitism and the number of host queens per nest, one could compare susceptibility both across and within species, and in colonies exposed to their parasites following experimental manipulation of queen number.

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